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CAMBRIDGE ZOOLOGICAL SERIES.

GENERAL EDITOR:—SIR ARTHUR E. SHIPLEY, SC.D., F.R.S.
MASTER OF CHRIST'S COLLEGE, CAMBRIDGE.

ZOOLOGY

CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, MANAGER
LONDON : FETTER LANE, E.C. 4

LONDON : H. K. LEWIS AND CO., LTD.,
136 Gower Street, W.C. 1
NEW YORK : THE MACMILLAN CO.
BOMBAY, CALCUTTA, MADRAS } MACMILLAN AND CO., LTD.
TORONTO : THE MACMILLAN CO. OF CANADA, LTD.
TOKYO : MARUZEN-KABUSHIKI-KAISHA

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ZOOLOGY

AN ELEMENTARY TEXT-BOOK

F21832

BY

SIR A. E. SHIPLEY, G.B.E., Sc.D.,
Hon.D.Sc. (Princeton), Hon.LL.D. (Michigan), F.R.S.
MASTER OF CHRIST'S COLLEGE, CAMBRIDGE

AND

E. W. MACBRIDE, M.A. (Cantab.),
D.Sc. (Lond.), Hon.LL.D. (McGill), F.R.S.
SOMETIME FELLOW OF ST JOHN'S COLLEGE, CAMBRIDGE
PROFESSOR OF ZOOLOGY IN THE IMPERIAL COLLEGE OF SCIENCE AND TECHNOLOGY, LONDON

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FOURTH EDITION

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1920

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SUBJECT SPECIALISATION

First Edition 1901.
Second Edition 1904.
Third Edition 1915.
Fourth Edition 1920.

PREFACE TO THE THIRD EDITION

IN the eleven years which have elapsed since the publication of the second edition of this Text-book the science of Zoology has made such advances that it has become necessary to re-write considerable portions of this book. The brilliant work of Dr Goodrich on the nature and development of nephridia has caused us to reconsider our position with regard to the nature of these organs and we have now confined the name nephridium to the excretory organs of Platyhelminthes, Nemertinea, Rotifera, Annelida and Amphioxus, and have no longer applied the term to the excretory organs of Arthropoda, Mollusca and Brachiopoda.

The chapter on Protozoa has had to be radically changed and we are indebted to Mr Dobell for valuable hints on this subject. The newer discoveries in the laws of inheritance are dealt with in the Introduction.

The chapters dealing with Platyhelminthes, Nemertinea, Rotifera and Nematoda have been moved to a position following Coelenterata and preceding Annelida. A short chapter on Gephyrea has been added and the chapter on Arthropoda has been largely rewritten. In the second edition detailed accounts of a type of Arachnida and of Insecta were given—to these we have now added a detailed account of the anatomy of the Crayfish as a type of the Crustacea, as experience has shown that only by the detailed study of types can the elementary student form clear images of Animals as "going machines." Indeed throughout the book we have endeavoured to avoid describing structure unless function was indicated at the same time.

In the section of the book dealing with Vertebrata many changes have been made. In the chapter on Fishes, we have endeavoured to bring clearly before the student's mind that the existing piscine population of the world's waters consists of two types of fish, the bony and the cartilaginous, and that the so-called Ganoids and Dipnoi comprise very few species, the last survivors of groups now nearly extinct. Sketches of the modern classification of Bony Fish and of Birds have been given so that the student may grasp to some extent the principles on which modern systematists proceed. Lastly, in the section dealing with Mammalia, considerable alterations were inevitable. Our largely increased knowledge of Theromorphous Reptiles has rendered untenable the view of the homology of the ear-ossicles of Mammalia formerly accepted by us, and the brilliant discoveries of Dr Andrews have settled the position of Elephants and Sirenia.

Besides those whose work we have mentioned above we owe thanks to Mr H. H. Brindley of St John's College, and to First Lieutenant J. T. Saunders of Christ's College, for much helpful criticism.

We are grateful for the reception which has been accorded to the second edition: we hope that the changes we have alluded to may increase the usefulness of the book.

A. E. S.
E. W. M.

1st January, 1915.

PREFACE TO THE FOURTH EDITION

ONLY a few changes have been made in the text of the last edition. Of these, those most worthy of mention are (1) the incorporation of Prof. Jennings' most interesting observations on the motion of Amoeba, which has involved the discarding of Prof. Rhumbler's hypothesis which was adopted in the third edition; (2) the inclusion of some new and interesting results on the physiology of the bivalve Mollusca; (3) the adoption of Dr Ridewood's results on the development of centra, which have narrowed the gap between the so-called arco-centra and chorda-centra; and (4) the rewriting of the section dealing with Human races in accordance with the views of Ripley, Elliot-Smith, Keith and other modern Anthropologists.

A. E. S.
E. W. M.

I wish to state that owing to pressure of duties as Vice-Chancellor, and other claims on my time, the Fourth Edition has been revised and seen through the Press by Prof. MacBride, and any improvements that appear in it are solely due to him.

A. E. S.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

a 5

CHAPTER I

INTRODUCTION

THE word Zoology (Gr. ζῶον, an animal; λόγος, a discourse) denotes the science which concerns itself with animals, endeavouring to find out what they are and how they came into being. It is a branch of the wider science of Biology (Gr. βίος, life, λόγος, a discourse)[1], which deals with all living things, plants as well as animals. Before any progress can be made with the study of Zoology, it is necessary to get clear ideas on two points: firstly, as to what is meant by life and living things; and secondly, as to how an animal is to be distinguished from a plant.

Life.

The idea implied in calling a thing living, is that in some respects its existence is similar to our own. Our own existence is the only thing immediately known to us, the standard with which we compare everything else. Every material object has certain points of resemblance to our bodies, inasmuch as all are composed of matter obeying the same laws of chemical affinity, gravitation, and so forth; it is necessary therefore to define the amount of resemblance which constitutes life. Now everyone knows that human beings grow, that is, increase in size at the expense of matter called food, which is different from themselves—and that further, they give rise at intervals to fresh human beings. These two fundamental characteristics—the power of growth and of multiplication—define life; everything that can increase its bulk by building up foreign matter into itself and that reproduces its like is said to be alive.

The idea originally underlying the word animal was a self-moving object as distinguished from a plant which was regarded as motionless[2] and this distinction, is broadly speaking true.

[1] This term is too well established to admit of alteration but it implies a mistranslation of βίος. This does not mean 'life' in the physiological sense but a period of life, a career, a life-time or circumstances of life, environment.

[2] It is true that to all general statements of Zoology, as to this, exceptions could be found. The rule followed in this book is to have regard only to the

The so-called movements of plants are almost always due to the growth of new parts and are not to be compared with the movements of animals which are the result of the alteration of relative position of fully formed organs.

Distinction between animals and plants.

Another fundamental difference between animals and plants is to be found in the nature of their food. Animals can only live on complex substances, not very different in chemical composition from their own bodies, and further, they can live on solid food. Plants, on the other hand, build themselves up out of carbon dioxide and other gases and out of water with a few simple salts in solution, and they only take in fluids or gases. There are, however, a certain number of living beings of extremely low and primitive character which combine the characters of animals and plants, and the question in which division they should be ranked is a matter to be determined only after a study of the special circumstances of each case.

It has been pointed out that our own existence is the original type from which the idea of life is derived. But we know ourselves primarily not as bodies in which growth and reproduction occur, but rather as conscious, thinking beings, and we are naturally inclined to imagine that animals at least, which not only grow and multiply, but in many other respects also resemble us, are likewise conscious. How far this belief is well-founded is open to serious question, if by consciousness we mean anything at all resembling our own inner life —the only consciousness we know anything about. The movements of the higher animals suggest that they experience the feelings of fear, anger, desire, etc., and it would be foolish to deny all similarity between them and man in these respects, but the habit which many people have of uncritically attributing purely human feelings to dogs, cats, horses, etc., is apt to lead us into serious error. Our forefathers went further than even we are inclined to do and supposed all natural objects, the sun, wind, trees, etc., to have spirits, that is, to be conscious. Since we can never learn much about the consciousness of beings with whom we cannot speak, zoologists content themselves with looking at animals entirely from the outside, without enquiring as to whether or no they are conscious[1]; animals are for

vast bulk of normal cases which gave rise to the *idea*. The reasons for classifying abnormal cases in one category or another are not general but special, and have to be considered in each case.

[1] The science of Comparative Psychology endeavours to make deductions about the minds of animals from their actions.

them bodies in which certain changes take place, changes such as growth, reproduction, movement, and others.

Protoplasm.

A close study of animals reveals the fact that though the chemical constitution of no two is exactly alike, yet all contain certain allied highly complex substances of very obscure chemical composition, known as proteids. These substances occur in the form of a thick, viscous solution in water; this is what is called by chemists a colloid solution or sol., which on very slight provocation passes into a gelatinous solid, or gel. This mixture of sol. and gel. is termed protoplasm (Gr. πρῶτος, first; πλάσμα, a thing moulded).

Further, it has been found that, so long as any sign of life is visible, this protoplasm is in a continual state of slow combustion, absorbing oxygen from outside and decomposing with the liberation of energy, and whilst some of the products of decomposition are cast off, others apparently reconstitute the original substance by combining with some of the materials of the food. The energy liberated is the cause of the movements which constitute the visible manifestation of life.

An animal then is only the more or less constant form of a flow of particles; it may be compared to a flame, which has a constant form, although the particles which compose it vary from moment to moment; unburned particles coming in at one end and the oxidised products escaping at the other.

Metabolism.

The deepest insight which can be obtained into the nature of life viewed as a series of changes in the shape and position of bodies reveals to us this continual chemical change as the ultimate cause of all manifestations of life. It is known by the convenient name of metabolism (Gr. μεταβολή, change, changing). The ultimate object of Zoology is therefore to discover the nature, cause, and conditions of the metabolism in the case of every animal; but the means of attaining this object are still to seek, and for the most part the zoologist has to be content with describing and comparing with one another the outer and visible effects of the metabolism in various cases.

The proteids, which form the essential basis of protoplasm, consist of carbon, nitrogen, hydrogen, oxygen, and sulphur; besides these elements phosphorus, chlorine, potassium, sodium, magnesium, calcium and iron are constantly found in the bodies of animals, and some of them are doubtless chemically combined with the proteid.

Phosphorus is a constituent of nucleic acid, a substance which in combination with proteid is characteristic of the nucleus (see p. 18). Proteids have a percentage composition which varies somewhat, though not widely, in different cases.

Carbon	from	50	to	55	per cent.
Hydrogen	,,	6·5	to	7·3	,, ,,
Nitrogen	,,	15	to	17·6	,, ,,
Oxygen	,,	19	to	24	,, ,,
Sulphur	,,	·3	to	2·4	,, ,,

The size of the molecules of which proteids are composed is undoubtedly a large one. It is difficult if not impossible to determine exactly how many atoms are contained in a molecule of a particular proteid because it is difficult to obtain one such substance in a pure condition free from admixture with others. The best determinations which have been made show however that at least 1000 atoms must be contained in the molecule. But the proteids known to the chemist are of course taken from the dead bodies of animals and are themselves to be regarded as products of the decomposition of the molecules which existed during life. The proteid as the seat of life has probably a decidedly different composition from the dead substance, and so to avoid confusion, we may call the living molecules biogens.

The biogen molecule is continually absorbing oxygen from the outside. This process is called respiration or breathing. It decomposes and some of the products are no longer capable of being built up again into other biogen molecules and are therefore got rid of, since otherwise they would interfere with the chemical action, just as accumulating ashes will eventually put out a fire. The process of ejecting these waste products is called excretion, the waste substances themselves, excreta, and the chemical changes which lead to their production, katabolism (Gr. καταβολή, deposition). The commonest excreta are water, carbon dioxide, urea, and uric acid; the last two substances contain nitrogen. But it is not necessary that in all cases excreta should be ejected. They may remain within the bounds of a mass of protoplasm; if they are removed from the sphere of the chemical action going on in the protoplasm this is sufficient. In some animals uric acid is stored in this way. Many of the excreta, though injurious if they remain in the protoplasm, are indirectly useful to the animal after ejection. Such useful excreta are called secre-

tions. Thus, all the hard skeletons of animals are really insoluble excreta. On the other hand, the gastric juice which digests the food in the human stomach, and the slime or mucus, which prevents a frog from drying up when taken out of water, are fluid excreta. A part of the body specially adapted to produce a secretion is termed a gland.

Other products of decomposition reconstitute, as we have seen, the original molecule by combining with the necessary elements from the food; this process is known as anabolism (Gr. ἀναβάλλειν, to put back or up) or assimilation. Inasmuch as, generally speaking, from the breaking up of one molecule more than one residue is produced capable of regeneration, there is an increase in the number of biogen molecules causing an increase in bulk of the protoplasm, or growth[1].

It is believed that both biogen and proteid molecules are of the nature of compound amino-acids. An amino-acid is an acid in which not only is the place of the central acid radicle corresponding to the sulphur in sulphuric acid or the phosphorus in phosphoric acid taken by a group of atoms containing carbon but this carbon group contains also NH_2 the radicle of ammonia. As a consequence an amino-acid can act not only like an acid in combining with an alkali but like an alkali combining with an acid—it is both an acid and a compound ammonia and has in consequence two hands—and owing to this circumstance it can combine with another group similar to itself by uniting so to speak its acid hand with the alkaline hand of the new group or vice-versa and so build up a complex chain.

The regeneration of the biogen takes place at the expense of the food. Taking in food is called eating, or ingestion. Since, however, the food must penetrate to every portion of the protoplasm it must be dissolved—a process effected by the chemical action of certain products of the decomposition of the biogens, known as ferments. The process is called digestion. The products of digestion must be assimilated; in order that this may be accomplished they are decomposed until quite simple substances are formed; in a word the amino-acid chain constituted by the ingested proteid is broken into its individual links. The casting out of an insoluble remnant of the food is called defaecation, and inasmuch as such remnants have never formed part of the biogen molecule,

[1] See Verworn, *General Physiology* (Engl. Edition), 1899, p. 486.

this process is carefully to be distinguished from excretion. The accumulation of excreta soon stops metabolism, whereas the intermission of defaecation need only interfere very slightly with metabolism.

Of the numerous solid particles found in protoplasm some are secretions, others are solid deposits of partly assimilated food, which act as reserve stores, others are indigestible remains or faeces. The fluid drops contained in it consist largely of water—some have in solution excreta or secretions; others contain the results of digestion.

Movement.

Animals, as we have seen, possess the power of executing movements; this power is exercised in order to seek their food and escape their enemies. However complicated these movements may be, they are all found to be dependent on the capacity of protoplasm to alter its shape, by suddenly contracting and then slowly expanding. By contraction is meant such an alteration of shape of the moving part as will tend to diminish its surface but not its bulk; that is, the contracting part tends to assume a spherical shape; by expansion, on the other hand, is meant an alteration of shape leading to increase of surface. A bird flies by contracting the muscles first on one side of the wing, then on the other; a fish swims by alternate contractions of the two sides of the fleshy tail. Any part of an animal fitted to execute movements more quickly in one direction than in another and so to bring about the movement of the whole animal, is called a locomotor organ. Protoplasm in which the power of contraction is highly developed is called muscle.

A contraction is the result of an explosive decomposition of the living substance; there have been a great many theories as to how the chemical change brings about the change of shape but, since all of them account for some of the facts and none of them for all, there is no need to mention any of them here.

The sudden chemical change which brings about contraction, although dependent on the unstable character of the biogen molecule, must be precipitated by some change occurring either in the living matter itself or in the surrounding medium, just as an explosion of gunpowder is not brought about without a spark. In either case the change causing the contraction is known as a stimulus, and the capacity of contracting under the influence of stimuli is known as irritability. Thus when a moth flies into a flame it is acting under the stimulus of light; when a hungry lion in the Zoological Gardens rises up and commences running violently

round its cage it is obeying the stimulus of hunger. In the first case we have to deal with an external stimulus, in the second with an internal one. Of course since all internal changes are ultimately due to changes in the surrounding medium,—e.g. hunger to a disappearance by digestion of the food in contact with the stomach,—the distinction between external and internal stimuli, though convenient, cannot be sharply drawn. The power of protoplasm to originate movement in consequence of internal changes is called automatism. In the case of external stimuli we can often observe that the disturbance caused at the point of application of the stimulus is propagated to widely different parts of the animal. Nerves contain protoplasm in which this power of transmission is powerfully developed.

Growth.

We have seen that at some period in the life of all animals when food is abundant, more living matter is formed than is broken down; in a word, that the animal increases in size, grows. But whereas volume increases proportionately to the cube of the length (or breadth), surface increases only proportionately to the square of the same dimension. Hence the amount of volume per unit of surface continually decreases as size increases, and thus the chemical action between the internal portions of the protoplasm and the surrounding medium, which can only go on through the surface, is slowed down; in other words, the activity of growth is checked and when a certain size is reached waste becomes equal to repair. At this stage there is a tendency for the protoplasm to divide into two or more pieces of smaller size. This division into smaller pieces is called reproduction, and it is a necessary result of growth. When an animal divides into two equal portions, the process is called fission, but when one portion is very much smaller than the other, the process is known as gemmation; the smaller portion is called the germ, and the larger the parent, since the latter is—somewhat illogically—regarded as identical with the original animal before division. A germ very rarely resembles the parent; usually it has to undergo a series of changes during growth by which it at last attains the shape of the animal which gave rise to it; this series of changes in shape and size is known as development.

Reproduction.

Reproduction in the higher animals is closely associated with another process called conjugation or sexual union. This process consists in the coalescence with one another of two portions of living matter. Conjugation probably

occurs in all animals, but the interesting thing about the higher animals is that they give rise to special germs of two kinds, called ova (eggs) and spermatozoa respectively, which cannot develop without first conjugating, one of the first kind uniting with one of the second. The lowest animals also produce such germs in many cases, but sometimes they are all alike and at other times they are different in size. Sometimes indeed they are almost indistinguishable from true ova and spermatozoa. The name gamete is employed therefore to designate conjugating germ cells irrespective of their size.

The ovum is devoid of the power of movement and has a larger or smaller amount of undigested or at any rate unassimilated food stored in it; this reserve material is called yolk. The spermatozöon, on the other hand, has no such reserve and is in consequence very much smaller than the ovum, but it possesses in nearly every case the power of movement by which it is enabled to seek and find the ovum. Reproduction, which thus requires conjugation before development can take place is called sexual reproduction. In most cases ova and spermatozoa are developed in different individuals. The individual giving rise to ova is called the female, that giving rise to spermatozoa is termed the male. In this case the species of animals is said to be bisexual. When both ova and spermatozoa are developed in the same individual it is spoken of as hermaphrodite.

Species.

It is obvious to the most casual observation that there is an amazing variety of animals in the world. Closer observation reveals the fact that while no two animals are exactly alike, all can be nevertheless sorted into a number of kinds called species, the individuals composing which—apart from the difference between males and females and difference due to age—resemble each other exceedingly closely. Where the observation has been made, it is always found that the members of a species conjugate freely with one another; and indeed this is assumed to be the case in every species; that is, we group a number of specimens into a species under the assumption that they can conjugate with one another, and that young like themselves will develop as the result. If this can be shown to be not the case, we conclude that a mistake has been made and that two or more species have been confounded with one another. It follows that the vast majority of species rest on provisional hypotheses; these hypotheses nevertheless possess a very high degree of probability, for by the

use of them only can the great resemblance between the individuals grouped together in the same species be accounted for. When, as occasionally happens, members of different species are fertile *inter se*, the offspring is termed a hybrid, and hybrids in the majority of cases are not fertile.

Heredity and Variation.

It has been pointed out, that whereas germs are in most cases exceedingly different from their parents, they nevertheless in process of growth come to resemble them. This tendency to reproduce the characters of the parent is called heredity. If the germ undergoes a large part of its development within a hard case, like a chick within the eggshell or in a cavity of the parent's body, it is called an embryo; if it moves freely about, it is termed a larva.

In the case of the development of an animal which has originated sexually, that is from the coalescence of two germs, the tendency is for it to assume characters intermediate between those of the two parents. Thus it is easy to see how sexual reproduction tends to annul the differences existing between members of the same species, by constantly producing means between them. When therefore a large number of individuals are found with very close resemblances, it is a reasonable supposition that the agent, which has caused this, is sexual reproduction; in other words, that they constitute a species. It is not however to be assumed that in every case conjugation results in the production of an animal exactly intermediate in character between the parents. In a large number of cases where father and mother differ from one another by some well-marked character unconnected with their sex the child resembles closely the father or the mother, a result denoted by the term prepotent applied to the parent which the offspring resembles. When however the children resulting from such a union are mated together, some of the grandchildren resemble one grandparent and some the other grandparent: three-fourths resemble the prepotent grandparent, and the character which they inherit is called the dominant character, and one fourth the other grandparent and the character which reappears in them is called the recessive character. When the grandparents differ in two characters, the same law holds with respect to each character, i.e. three-fourths of the offspring resemble one grandparent and one fourth the other—but not all the same children fall into the same group in the case of each character, and so some children inherit the dominant character from one parent and the recessive from another, and thus

two new types are formed. Individuals belonging to the same species which differ from one another in well-marked characters are termed varieties, and the laws governing the inheritance of character when two varieties are mated together were worked out by an Augustinian monk named Mendel, whose work has been repeated and extended by a flourishing school of modern investigators. These laws show how when two varieties of a species exist, new varieties can result from their crossing, but they throw no light on a question of cardinal importance, how the varieties themselves came into existence in the first case. In a few cases however, the sudden appearance of these new varieties has been actually recorded. In all these cases the new variety may be described as a cripple; it is characterised by the loss or imperfect development of some character found in the normal form. A variety is to be discriminated from a race; a race is a subdivision of a species occupying usually a definite area and discriminated from neighbouring races by a multitude of small characters.

Branches of Zoology.

It is obvious that so vast a science as Zoology must be divided into various branches, since the different questions it seeks to solve require that special attention should be given to each side of the subject. Thus, the nature and conditions of the metabolism and the mechanism by which movements are effected, etc., constitute the subject-matter of Physiology; the investigation of the structure of individuals and of the differences in structure between the various species and the search for the causes of these differences is termed Morphology; whilst Bionomics is the name given to the study of the means whereby an animal obtains its food and orders its life, in other words, of its habits. But it must be remembered that all such divisions are purely arbitrary, and indeed no great progress can be made in any one department if the others be ignored. Bionomics, when followed to its sources, passes into Physiology, and in trying to explain the different structures studied in Morphology constant recourse must be had to both Physiology and Bionomics.

Of all divisions of the subject, that of Physiology has been most neglected; it has indeed been studied systematically only in the case of man and of a few of the higher animals. Hence this work will be mainly concerned with the questions of Morphology and Bionomics. Of these questions, by far the greatest is the problem how the distinctions between the various species are to be explained. The question of the "Origin of Species" involves nearly all others in Zoology.

Classification.

The distinctions between species are of very different degrees, so that for convenience species closely resembling each other are collected into genera—genera into families—families into orders—orders into classes—and classes into phyla. These are the names in commonest use, but often the nature of the subject requires the introduction of further grades of difference, and the number of grades actually employed depends to a large extent on the point to which the analysis is pushed.

Origin of Species.

The only theory of the origin of species which has so far commanded any considerable agreement amongst naturalists is the famous theory of Charles Darwin. According to this theory, the resemblances between a number of living species are due to the fact that these species are descended from a common ancestral species which possessed the common features as characters of its own. Therefore, the degree of likeness between species is the expression of a nearer or remoter blood relationship, and it logically follows that, since no part of the animal kingdom is without resemblances to the rest, if we recede far enough in time we reach a period when all the animals in the world constituted one species.

To a certain extent Darwin's theory was only the expression of ideas that had first occurred to Greek philosophers, and had in one form or other been put forward by many naturalists before him. His special merit lies in that he pointed out various processes at present going on in nature which must lead to the modification of species. He recalled attention to the well-known fact which we have just discussed, that although the offspring in general resemble the parents, yet this resemblance is never exact, and further that the young of one brood often differ quite perceptibly from one another, and that these differences are often inherited by the offspring of the individuals showing them.

Again, another fact well-known but usually ignored, was emphasised by Darwin: viz., that if the state of the animal population of the globe remains fairly constant, out of all the young produced by a pair of parents during their lifetime on an average only two will survive, since if more were to live the species would inevitably increase in numbers. Hence since each animal tends to multiply at a rate at which if unchecked it would soon overrun the globe, a competition must result between the members of each species both for food and in the escape from enemies, as a result of which the "fittest" will survive. So long as the surroundings of the species

remain the same, this struggle for existence will only weed out those individuals least perfectly adapted to their environment, so that the species will be kept up to a high level of adaptation to its surroundings. This elimination of imperfect individuals which results in the survival of the fittest is known as Natural Selection. Thus we can well imagine that if white-haired individuals turned up amongst hares, they would be more conspicuous and hence more easily discovered by the animals which prey on hares. If however the circumstances of a species change, a different class of individuals will survive. For instance, if for the greater part of the year the country inhabited by the hares were covered by snow, as is the case in the North of Canada, the whitest-haired individuals would have the best chance, and from generation to generation would be selected until the colour of the hare was totally changed. The progressive modification of species by the agency of natural selection is called evolution. If the modification tends towards simplification of structure it is called degeneration, if on the contrary it tends towards great complexity it is spoken of as differentiation.

So far the theory shows how a species will become slowly modified as its surroundings change. But it has been postulated that distinct species have arisen from the same ancestors. It is of course not difficult to see that if a species is distributed over a wide area the conditions in different portions may vary independently of one another, and hence the species may become modified in one place in one direction and in another situation in a different direction by the agency of natural selection. So long however as the species inhabits a continuous area this tendency to split up into divergent groups will be checked by inter-breeding between the sections of the species which are thus becoming modified in different directions. But if through geographical changes the species becomes divided into groups of individuals cut off from access to another, then no inter-breeding can take place and in time two species will be formed. Thus when birds have been blown far out to sea and have colonised a distant island they have often given rise to a new species. The same result may be brought about by the sea overflowing a part of the area inhabited by the species, an event which we know from geology to have often occurred. The important fact to be borne in mind is that at bottom the evolution of several species out of one is due to the formation of colonies, and that the same causes which have led to the differences between the American and the Englishman have acted again and again in the world's history so

as to produce the marvellous variety of species inhabiting the globe, the only difference between human and animal colonies being that, in the latter case, the divergence has become so great that animal colonists will no longer breed with the original race. Thus, accepting Darwin's theory, we find it possible to give a rational explanation of those resemblances between animals which are expressed in a system of classification[1]. If the theory be rejected these resemblances are pure figments of the human mind, and the species must be regarded as just as independent of one another as are the chemical atoms. Hence since it is a choice between this explanation or none, the Darwinian theory of gradual evolution is accepted by the overwhelming majority of naturalists. Differences however exist as to the nature and origin of the variations out of which evolutionary change is built up. It has been shown that the minute differences between brothers and sisters on which Darwin relied are usually non-inheritable. Larger variations occurring at rarer intervals are strongly inherited but as already mentioned these are of the nature of pathological defects and are utterly unlike the marks which divide natural species. Of quite recent years some evidence has been brought forward to show that increased use which leads to increased size produces inheritable effects. The selection would then operate in causing the survival of those that responded most actively to the needs imposed by the environment.

One or two interesting consequences follow from the acceptance of this theory. The structural features of animals are to be regarded as adaptations to their surroundings, since they have been built up by natural selection. Hence an isolated resemblance in a particular feature between two species need not necessarily indicate that this feature was present in the common ancestral species, for similar surroundings may have evolved a similar modification in two animals only remotely related. Such similarities are called homo-

[1] Most of the names employed in classification were in use before Darwin's views were accepted. The word phylum (Gr. φῦλον, tribe or stock) is however an exception. This term expresses the central idea of the evolution theory, and its proper use is to denote the whole of a group of animals characterised by having the same ground-plan of structure and believed to be the descendants of a common ancestor, from whom no other living animals are descended. The essential feature about a phylum is its isolation, in the present state of our knowledge, from other phyla. Of course it is believed that at bottom all living beings constituted one phylum, but there are enormous differences in structure which can only be bridged by imaginative hypotheses.

plasy, whereas resemblances believed to indicate blood-relationships are grouped under the term homology.

Again, the immature forms of some animals are found to exhibit strong resemblances to the adults of others, and the eggs of all the highest animals show the strongest general resemblance to the simplest animals—the so-called Protozoa (Gr. πρῶτος, first, ζῶον, animal). If these resemblances are to be interpreted in the same way as those prevailing between adults—and it is illogical to refuse to do so—then we are driven to conclude that most animals in their development pass through stages when they exhibit many characters once possessed by their ancestors, commencing at the stage of the Protozoa. Some of these latter animals, since they are about as simply constructed as we can imagine living matter to be, may be looked on as slightly modified survivors of the first animals which appeared on the globe.

This method of interpreting the changes which occur during development is what is known as the Recapitulation Theory, because during Ontogeny (Gr. ὄν, ὄντος, being) or the development of the individual, nature recapitulates to some extent the development of the species in past time, Phylogeny (φῦλον, a stock, a race). There are, however, a great many other factors which have modified development, and the determination of these and their separation from the hereditary factor is a task requiring careful study and one which is as yet far from complete.

CHAPTER II

PHYLUM PROTOZOA

The Protozoa are distinguished from all other animals (1) by the fact that when they produce germ cells or gametes the whole animal breaks up into them, (2) by the fact that the protoplasm of the body is never differentiated into tissues nor exhibits cellular structure (see p. 30)[1]. The higher animals are often grouped under the name Metazoa (Gr. μετά, after; ζῷον, an animal) in order to contrast them with the Protozoa, but whereas the Protozoa, since they have a common structural ground-plan, constitute a phylum in the sense defined in the last chapter the same is by no means true of the Metazoa. Hence the name Metazoa does not denote a phylum but is a mere convenient collective term.

The term Invertebrata is also a mere collective name; it is employed to designate all animals which do not belong to the phylum Vertebrata. Like the name Metazoa its convenience in promoting terseness of expression is its only justification. The Protozoa are thus Invertebrata and the Vertebrata are Metazoa.

The phylum Protozoa includes the simplest and lowest members of the animal kingdom. With few exceptions the members of this phylum are too small to be seen by the naked eye, and yet many of them are of great importance in the economy of nature.

In order to fix our ideas we may select one of the simplest Protozoa as a type for examination. *Amoeba*, sometimes called the Proteus animalcule, from its power of continually changing its shape, is found in the mud at the bottom of ditches, ponds and pools of stagnant water. There are several species varying somewhat in size included under the generic name *Amoeba*, all of them, however, are so small as to

Amoeba.

[1] These statements are true of the vast majority of animals classed as Protozoa. The exceptions are for convenience classified as Protozoa, but it seems to the authors that in the light of a fuller knowledge they may turn out to be survivors of that great series of forms which must, if the evolution theory be true, have intervened between the Protozoa and the Metazoa.

necessitate the use of a microscope for their examination. When magnified an *Amoeba* appears like a small, almost transparent lump of jelly, in which we can distinguish a thin outer rind and inner substance. The first, called the ectoplasm, is almost absolutely transparent, the second, called the endoplasm, has usually a grayish tinge, due to the presence of minute solid particles or granules, and is therefore described as granular. Often indeed, good sized objects of various shapes and generally of a green or yellow colour, can be seen in the endoplasm; these are the undigested remains of the microscopic plants which the animal has

FIG. 1. *Amoeba proteus* × 330. From Gruber.

1. Nucleus. 2. Contractile vacuole. 3. Pseudopodia, the dotted line points to the clear ectoplasm. 4. Food vacuoles. 5. Grains of sand.

eaten and are surrounded by bubbles of water, termed food-vacuoles. *Amoeba* frequently engulfs particles of sand, though for what purpose is unknown; possibly in order to render itself less palatable to animals which might eat it. If the *Amoeba* is healthy we shall see it move. The transparent ectoplasm slowly sends out a projection, and then the granular endoplasm flows into it. As of course the size of the animal does not alter, when a process is thrust out in front, the rest of the animal must follow it by shrinking away behind.

These projections are called by the awkward name of pseudopodia (Gr. ψευδής, false, πόδιον, a little foot); the adjective

pseudo- implies that they are not fixed organs like our own limbs, but are made at any part of the surface of the body. When *Amoeba* comes across anything it desires to eat, it throws out pseudopodia on each side of it; these then unite beyond the object, and so the latter becomes engulfed, so to speak, in the body of the animal, where it is digested. It may thus be said, that *Amoeba* flows round its prey. Once the prey is inside, it is surrounded by a drop of water poured out of the surrounding protoplasm or enclosed with the food. There is probably some substance secreted into this water which acts on the prey and dissolves it. The most recent and careful study of *Amoeba* by Jennings has convinced him that the throwing out of pseudopodia and movement generally are due to changes in the ectoplasm, the endoplasm being passive. Local contractions in the endoplasm seems the most probable cause and when we study a slightly higher grade of animal we shall find that these contractions are carried out by specialised threads called myonemes. It is hard to resist the conviction that in the ectoplasm of *Amoeba*, there is something corresponding to myonemes although we cannot see them. The ectoplasm is a permanent skin; only where it surrounds a food vacuole is it ever dissolved. The comparison of *Amoeba* to an oildrop originally made by Butschli has proved baseless.

One of the most marked features in which *Amoeba* differs from other animals, from ourselves for instance, is, that it possesses no separate parts or organs, such as stomach, heart, lungs, etc., fitted to perform the separate vital actions, or functions as they are called. It breathes, that is, absorbs oxygen and gives off carbon dioxide all over the body; and it likewise excretes, that is, gets rid of the oxidised protoplasm, at all points of the surface. If, however, we are so fortunate as to come across a large *Amoeba*, which is at the same time comparatively clear of granules, and is moving only sluggishly, we may be able to make out two definite objects in the endoplasm. The first of these is called the contractile vacuole (2, Fig. 1); this is a clear round space, which slowly enlarges and then suddenly vanishes, and then reappears in the same place and goes through the same series of changes. It has been suggested that the cause of this appearance is that at a certain point in the endoplasm a substance is produced by katabolism with a strong affinity for water; this substance attracts to itself from the surrounding protoplasm water, carrying in it the soluble waste products, in

fact draining the protoplasm and forming a drop. This drop swells until it, so to speak, bursts the covering of protoplasm separating it from the outside water; the space it occupies then collapses, but as soon as the fluid has escaped the rent in the protoplasm joins up again, and as the excretory process continues the drop of fluid again accumulates.

Nucleus.

The other object which we may perceive is the nucleus. This is a spherical body consisting apparently of the same kind of material as the endoplasm, only slightly denser (1, Fig. 1). If we, however, kill the animal by running in some iodine under the coverslip, the nucleus stands out at once in contrast to the rest of the protoplasm by its property of taking up more iodine and appearing stained a much deeper colour, and this happens in the case of any *Amoeba*, whether we have been able to see the nucleus whilst it was living or not. Close examination by means of high powers reveals the fact that only part of the nucleus is concerned in taking up stain. This part—which is called chromatin—in *Amoeba* usually takes the form of a clump or mass which is bathed in a fluid, the nuclear sap, contained within a membrane, the nuclear wall. Chromatin contains phosphorus in combination with a peculiar compound known as nucleic acid. The material contained in the nucleus is an essential part of the body: when an *Amoeba* is deprived of it, metabolism within the protoplasm slackens and finally stops. Nearly all living things, animals or plants, possess one or more nuclei, though in some rare cases the essential nuclear material is dispersed throughout the protoplasm. The bigger the plant or animal, the more nuclei it possesses. The so-called "Flowers of Tan" (Mycetozoa), which creep over the hides in tan-pits, are some of the few Protozoa which are distinctly visible to the naked eye; they may be compared to gigantic *Amoeba* with branching pseudopodia, and they have thousands of nuclei. In the case of certain Protozoa it has been proved that if the animal be broken in pieces, those bits which contain a nucleus can repair themselves and continue to live, and eventually grow up to form an animal like the one of which they are fragments; but those bits which contain no nucleus, though they continue to live for a short time, have no power of feeding themselves nor of growth. On the other hand if the nucleus be freed from protoplasm it dies; life depends on the mutual reactions of protoplasm and nucleus.

The reproduction of *Amoeba* ordinarily takes place by the simplest conceivable process; the animal divides itself into two. This

process is called fission. and it is found that the nucleus always divides into two before the body as a whole shows any signs of the process. When *Amoebae* are exposed to unfavourable conditions, such as the drying up of their surroundings, they have the power of enclosing themselves in a cyst. They draw in all their pseudopodia and assume a spherical form, and the cyst appears as a membrane on the outside which then thickens. Once enclosed within its cyst, *Amoeba* can be blown about like a particle of dust, and in this way we can account for the fact that we sometimes find *Amoeba* in infusions, that is, solutions made by allowing some animal or vegetable matter to stand in water exposed to the air. If we put some hay or meat into perfectly pure water and expose it to the air, it will putrefy; this is due to the development of minute microscopic plants called Bacteria, the spores of which are carried by the air: at a later stage, various Protozoa and sometimes *Amoebae* will appear. At one time it was supposed that both Bacteria and Protozoa were spontaneously developed out of the dead meat, but it has been shown that if the water and meat be boiled, so as to kill any spores which may be in them, and the mouth of the vessel plugged with cotton-wool whilst steam is issuing, so that the air penetrating from outside through the interstices of the wool has all the spores it may carry strained off before it comes in contact with the water, neither Bacteria nor Protozoa will appear. The cyst which invests the body of the *Amoeba* is the first instance we have met with of what is called a secretion. A secretion has already been defined as dead substance which is of use to the animal, and which is produced by the decomposition of protoplasm.

Reproduction and Encystment.

In one or two cases an *Amoeba* enclosed within its cyst has been seen to break up into a number of rounded germs which were eventually set free by the breaking of the cyst and each of which then took on the form of a minute *Amoeba*. This process is called sporulation and the germs to which it gives rise spores. It is unknown whether every species of *Amoeba* sporulates and if so under what conditions this occurs.

When we were describing the endoplasm of *Amoeba* above, we called it granular, owing to its containing solid particles. It must however be remembered that the endoplasm is a colloid solution or sol. whilst the ectoplasm is a "gel." In the sol. are dissolved the oxygen necessary for life and the carbon dioxide which has

resulted from the oxidation of the living matter, and so we can understand how the chemical action which is essential to life can go on in every part of the living substance, remembering the fundamental chemical maxim "corpora non agunt nisi soluta." The granules are temporary deposits in a solid form, either of matter resulting from katabolism, or of nutritious matter not yet assimilated.

We must now glance at some animals allied to *Amoeba*, in order to gain some idea of the group Protozoa as a whole.

Lobosa.

Difflugia and *Arcella* are both found in the mud of pools and ponds; they resemble *Amoeba* in general structure but differ from it in being provided with shells. In consequence of having these they are only able to put out pseudopodia at one spot, the mouth of the shell. The shell of *Difflugia* is composed simply of grains of sand stuck together with a secretion; it has the shape of a pointed egg with the thick end cut off (1, Fig. 2). *Arcella*, on the other hand, makes its shell entirely out of its own secretion; this is colourless when thin, but as the animal grows older the shell becomes thicker and acquires a characteristic brown colour, and we are enabled to recognise that it consists of chitin. This is really a name for a class of substances which are constantly met with in the animal kingdom and which according to some investigators are allied in composition to uric acid. Out of chitin, for instance, all insects construct their hard cases. It seems probable, that the self-destruction of protoplasm, which results from the ordinary vital functions, may in many cases give rise to chitin, so that perhaps in *Arcella*, the shell is at once a protection and the ordinary excretion. The shape of this shell is like a watch-glass with a flat lid resting on it, and in the middle of the lid there is a round hole through which the pseudopodia come out. Sometimes gas bubbles (7, Fig. 3) can be seen in the body of the animal, which tend no doubt to balance the weight of the shell. *Arcella* possesses two so-called primary nuclei and in

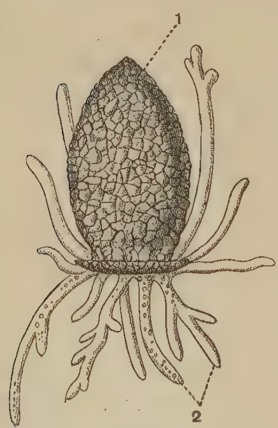

FIG. 2. *Difflugia urceolata* × 100. After Leidy.

1. Shell composed of particles of sand containing body of the animal. 2. Pseudopodia.

addition a cloud of minute nuclear particles known collectively as a chromidium. The chromidium consists of material emitted by the nucleus of the germ before it divides into the two nuclei seen in the adult. When *Arcella* reproduces a large part of the protoplasm emerges from the shell, each primary nucleus then divides into two, and two of the daughter nuclei take up their positions in the outside mass which is then cut off as a new *Arcella*. At other times the primary nuclei dissolve and disappear, and the protoplasm aggregates

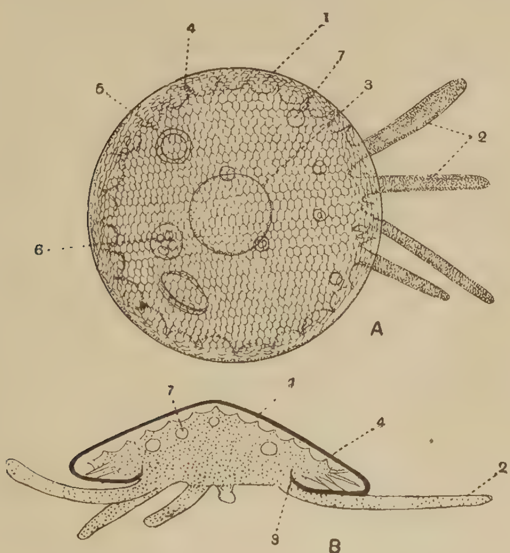

FIG. 3. *Arcella discoides* × 500. From Leidy.

A. Seen from above. B. Seen from the side, optical section. 1. Shell. 2. Pseudopodia. 3. Edge of opening into shell. 4. Thread attaching animal to inner surface of shell. 5. Nucleus. 6. Food vacuole. 7. Gas vacuole.

itself as spherical lumps round the minute particles of the chromidium which form secondary nuclei. These ball-like masses are spores; they are extruded one by one from the shell and at first they put out stiff pseudopodia like *Actinophrys* (see below). These minute germs unite in pairs and the compound organism is called a zygote and grows up into a young *Arcella*. The union of two germs so as to form a single germ which grows vigorously is the simplest form of the

sexual process. Germs which unite with one another are termed gametes.

The Protozöon *Gromia* possesses a thin membranous shell, shaped somewhat like that of *Difflugia*: but the animal shows two important differences; first, the protoplasm of which the body is composed, besides filling the shell, extends in a thin layer all over its outer surface (2, Fig. 4), and secondly, the pseudopodia, which are given off from this layer, are thin and delicate threads which join and interlace with each other so as form a network. *Gromia* seizes its prey by entangling it in these fine pseudopodia; these then flow together and form a little island of protoplasm surrounding the captive, which is thus digested quite outside the main part of the body; the products of digestion being carried along the pseudopodia into the protoplasm which is inside the shell.

We may next consider a rather larger Protozöon allied to *Gromia* and like it possessing a shell, which however is composed not of chitin but of calcium carbonate. The name of this animal is *Polystomella* (Fig. 5). Like *Gromia* it possesses delicate interwoven pseudopodia which spring from the whole surface, since there is a thin layer of protoplasm covering the outside of the shell as well as the main mass inside it. Unlike *Gromia*, however, *Polystomella* has a shell which is perforated by a large number of minute holes, through which pass cords of protoplasm, connecting the inner and outer parts of the animal. *Polystomella* is therefore a typical example of the Foraminifera (Lat. *foramen*, a hole; *fero*, to carry), a class which includes countless varieties of microscopic shells, generally composed of calcium carbonate, less frequently of flint (silica). The Foraminifera show essentially the same method of reproduction as *Arcella*. For this reason, as well as because many of the genera classed by naturalists as Foraminifera have imperforate shells, the name Thalamophora is preferred, which includes *Arcella* and *Difflugia* as well as the so-called Foraminifera. The differences of structure between *Polystomella*, *Difflugia* and *Arcella* implied in the fact that the two latter have no layer of protoplasm outside the shell and that their pseudopodia are blunt are considered to be of less importance than the possession of a skeleton and a chromidium. In order to distinguish them from the Thalamophora the various varieties of *Amoeba* are called Amoebidea. If we examine the shell of *Polystomella* with the low power of a microscope, we shall see that it is shaped like a rather flat snail shell or the shell of the Pearly Nautilus. If, however, we dissolve

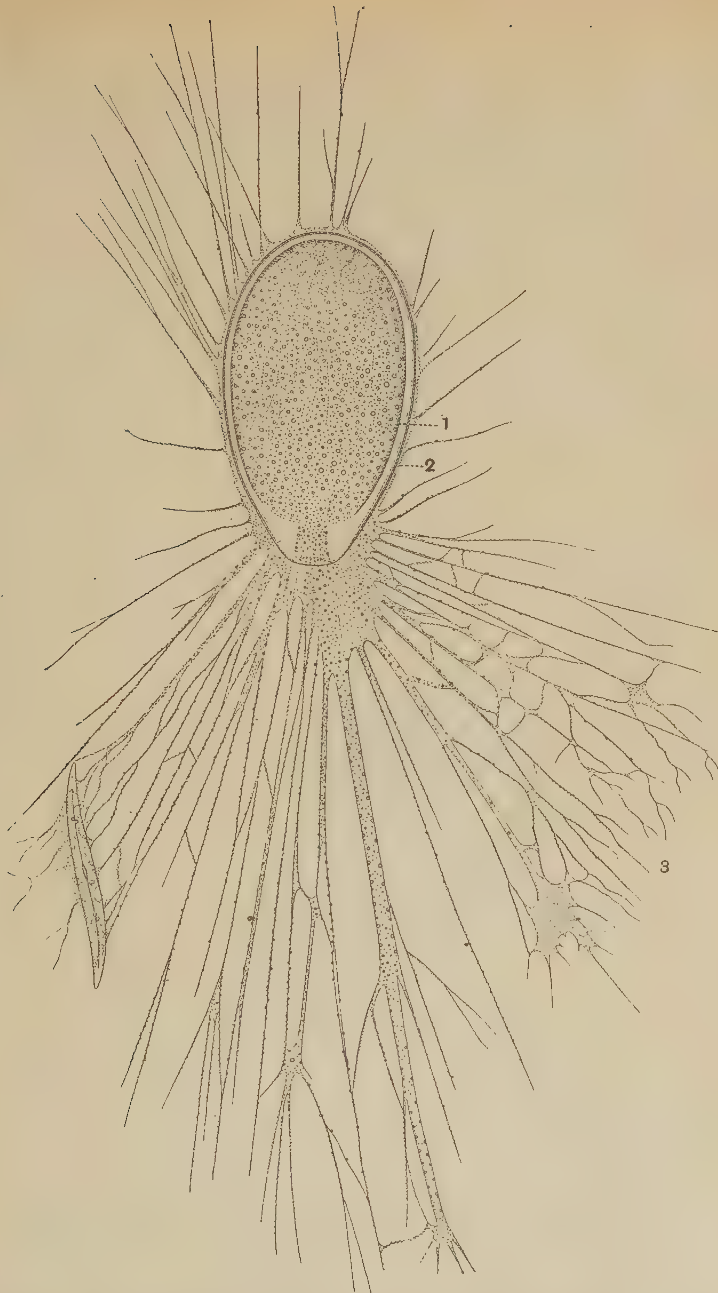

FIG. 4. *Gromia oviformis* × 250, but the pseudopodia are less than one-third their relative natural length. From M. S. Schultze.

1. Shell. 2. Protoplasm surrounding shell. 3. Pseudopodia, fusing together in places and surrounding food particles such as diatoms.

away the shell with dilute acid so as to expose the proper body of the animal, it will be seen that this is made up of separate parts

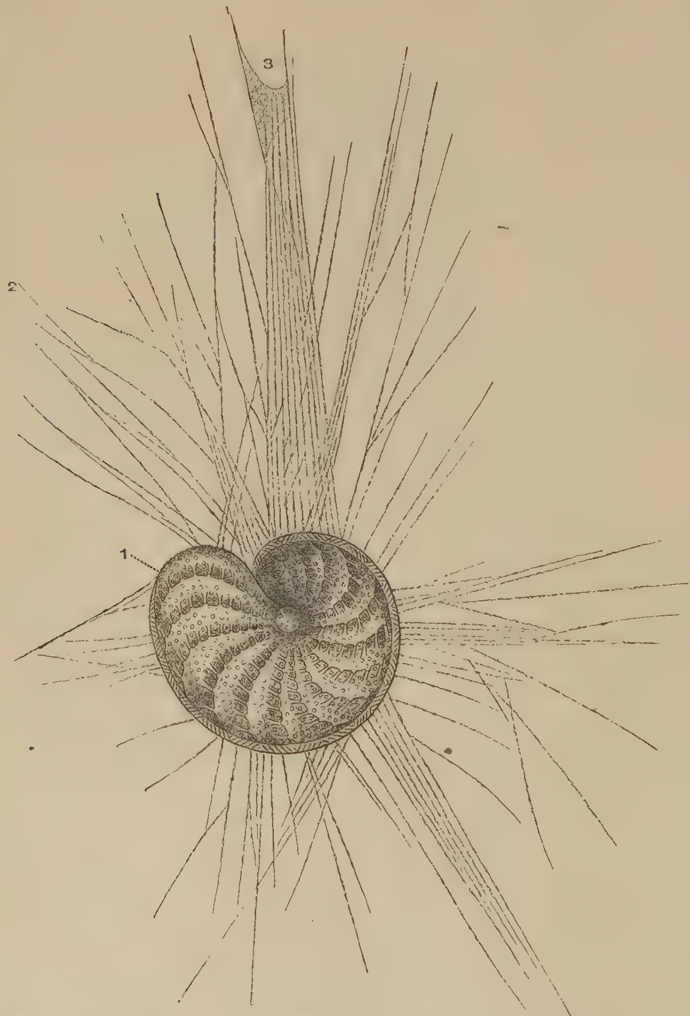

FIG. 5. *Polystomella crispa*. Highly magnified. After M. S. Schultze.
1. Shell. 2. Pseudopodia. 3. A mass of protoplasm formed by the fusion of pseudopodia.

each united to the next one by two or three little bridges of protoplasm, and arranged one behind the other in a spiral series. This is the first example we have met with of the repetition of similar

parts in a definite order, but upon this principle of the repetition of similar parts the bodies of the most complicated animals are built up. It is no doubt fundamentally the same thing as reproduction, only that the various units which are produced, instead of separating from each other and leading separate existences, remain connected, and, as we say, are co-ordinated to form an individual of a more complex kind. In *Polystomella* the various parts are called chambers; a name which properly belongs, and was first applied to, the segments of the shell enclosing them. It is worthy of note that it is only the protoplasmic body of *Polystomella* which shows this composition out of definite units arranged in a definite order; there may be one large nucleus or a considerable number of smaller nuclei, but they are not arranged in correspondence with the chambers.

The Thalamophora, which, like *Polystomella*, have compound shells, are very numerous and include an immense variety of forms, the variety being brought about by differences in the number of chambers and the way they are arranged in series. They almost all live in the sea; some, like the two we have described, creep about amongst the sand and débris at the bottom of pools or other places where the water is quiet; many others float at the surface of the ocean, the protoplasm which clothes the outside of the shell having numerous vacuoles filled with fluid probably less dense than the sea-water, and thus serving as floats. In such inconceivable myriads do these floating Thalamophora exist, that their empty shells form thick banks of impalpable white chalky mud at the bottom of the ocean, and the familiar white chalk of our English cliffs and hills is largely made up of the shells of Thalamophora.

When such a form as *Polystomella* is about to reproduce by fission the protoplasm emerges from the old shell and divides repeatedly into a number of pieces each as large as the central chamber of an ordinary individual. These then secrete round themselves shells and begin to bud off new chambers and gradually acquire the size and shape of adults. When on the contrary *Polystomella* forms gametes, the nucleus seems to break up into a chromidium like that of *Arcella*, which is dispersed throughout the protoplasm, and the protoplasm whilst still within the shell divides into a large number of small rounded pieces, each of which contains one of the minute fragments of the nucleus. These rounded bodies are gametes; they acquire hair-like projections called flagella which can be moved to and fro and by means of which they can

swim. The gametes escape from the shell and move freely about, they coalesce with one another in pairs, and the resultant mass or zygote acquires a shell and begins to bud off new chambers. Since in spite of the fact that the zygote has resulted from the union of two gametes it is much smaller than a product of ordinary fission, the adult resulting from the growth of a zygote is distinguished from that resulting from fission by the small size of the initial chamber. Hence we can distinguish a microspheric form resulting from the development of gametes from a megalospheric form resulting from fission. Lister has shown that in *Polystomella* there is an alternation of fission and formation of gametes, but that more than one generation which undergoes fission intervenes between two which form gametes.

Radiolaria.

We may pass now to the consideration of some Protozoa which show a good deal of resemblance in many points to the Thalamophora, though they have very marked peculiarities of their own. These are the Radiolaria; they have delicate threadlike pseudopodia, and their protoplasm is divided into two parts—an inner and an outer—by a membranous case pierced with pores, through which the two parts of the body are connected with each other. This case, the central capsule, may be compared to the Thalamophoran shell, and the protoplasm outside it gives rise to the pseudopodia, but the interesting fact is that these Radiolaria have in addition to this another skeleton composed not of chalky—calcareous—but of flinty—siliceous—substance, as are also some of the shells of the Thalamophora. This flinty skeleton may consist simply of isolated needles sticking out on all sides from the centre; oftener, however, it consists of a beautiful basketwork as in *Heliosphaera inermis* (Fig. 6), and sometimes we find several of these baskets one within the other, like the Chinese ivory ball. The Radiolaria, like the free-swimming Thalamophora, have a vacuolated outer protoplasm, and often drops of oil in the inner protoplasm; these structures serve to sustain them and they are found floating at the surface of the sea amongst Thalamophora. At the bottom, in medium depths, their flinty skeletons, though mixed with the calcareous shells of the Thalamophora, do not affect the general character of the chalky mud (called the *Globigerina* ooze, from the name of one of the commonest Thalamophora found in it), but at greater depths, owing to the enormous pressure, the quantity of carbonic acid dissolved in the water increases very much (on the same principle that the pressure inside a soda-water

bottle keeps the gas dissolved) and all the shells composed of chalky matter are dissolved, only the flinty skeletons being left. The bottom mud here entirely changes its character and is called Radiolarian ooze. When Radiolaria reproduce the chromatin of the nucleus breaks up into a chromidium from which secondary nuclei are formed. Round these nuclei spore-like masses of protoplasm aggregate themselves and these escape as isospores, each of which has two vibratile filaments or flagella (see below). At other times some only of the chromatin of the primary nucleus breaks up into a chromidium, the rest divides into larger pieces and thus anisospores, that is spores of two sizes, large and small, are formed, each of which possesses two flagella but one of these encircles the protoplasm like a belt. It is probable that these spores must

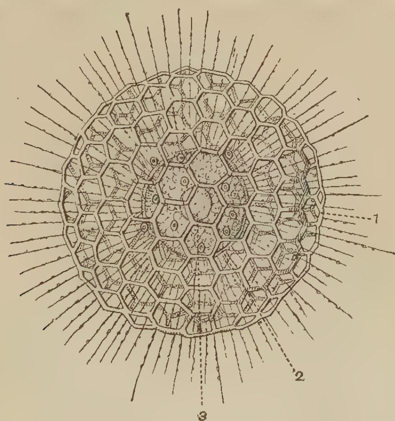

FIG. 6. *Heliosphera inermis* × 350. From Bütschli.
1. Skeleton. 2. Central capsule. 3. Nucleus.

conjugate to form a zygote before they can develop; in a word that the isospores are asexual germs but that the anisospores are gametes.

Mycetozoa.

The next group of Protozoa to be considered is a very remarkable one, including the largest forms known. The so-called "Flowers of Tan" (Mycetozoa) are brightly coloured patches, which may be seen on the surface of the oak-bark used in tan-pits. Similar patches may be seen on old tree stumps and on the surface of beanstalks which have been wet for a considerable time. These patches under the microscope are seen to resemble enormous *Amoebae* with thin branching pseudopodia, which are apt to join one another to form networks, although these

networks are much coarser than in the case of the Thalamophora. The fluid endoplasm is seen to have a regular flow alternately backwards and forwards in these pseudopodia; the movement of the whole mass in any direction being due to the predominance of the forward flow over the backward, or vice versa. When stained the protoplasm is seen to include thousands of very small nuclei. The name Mycetozoa literally means Fungus animals (from Gr. μύκης, a fungus, ζῶα, animals). They are also often called Myxomycetes—literally Slime-Fungi, both names having been suggested because their special mode of reproduction leads some naturalists to consider them to be plants. Their power of encystment is very marked, for the slightest tendency to drought calls it into action, and then a mass will break up into numerous cysts, which will remain perfectly passive until wetted. Before reproduction, the same process occurs, but the nuclei multiply by division and then fuse in pairs with one another; the contents of the cyst then become aggregated round these final nuclei as rounded germs called spores—which acquire walls of cellulose, a constant product of plant life. Such spores are called chlamydospores. In one group of the Mycetozoa known as Endosporeae a portion of the plasmodium swells up so as to form a rounded mass on a stalk which is termed the sporangium and which encysts itself. In another group lobe-like fingers grow out from the plasmodium, from the apices of which spores are constricted off one by one. These are called the Exosporeae. Some of the protoplasm not used in the formation of spores forms long threads of cellulose, called collectively a capillitium, which when wetted expands and so expels the spores. The appearance of cellulose was the only justification for regarding these animals as in any way allied to plants, and it is known that cellulose is quite a constant product in some groups of animals. The contents of the spore escape as a germ propelling itself by a flagellum (B and C, Fig. 7), the germ itself being termed a flagellula. This thread is soon withdrawn and the germ takes on the form of a small Amoeba and is then called an amoebula (D, E, and F, Fig. 7). Many of these amoebulae coalesce to form the adult form, which is called the plasmodium (G, Fig. 7), a name given to the result of the fusion of a number of originally separate animals.

Heliozoa.

The Sun animalcules, or Heliozoa (Gr. ἥλιος, the sun), which inhabit, with few exceptions, fresh water, were formerly confounded with the Radiolaria, but they are in reality very different from these. They are spherical in shape and

have a large number of stiff pointed pseudopodia sticking straight out all round them, like the conventional rays in pictures of the sun. The common and scientific names are taken from this circumstance. Since these animals float about, it is not surprising to find much the same structure in the outer protoplasm as we found in Radiolaria and the floating Thalamophora. The pseudopodia are different in character from those of the Thalamophora, since they do not interlace, nor do they run together when they seize prey; the captured food is simply pressed in towards the body by the

FIG. 7. Various stages of *Chondrioderma difforme*. From Strasburger.
A. Flagellula leaving cyst. B & C. Flagellulae. D young and E older amoebulae. F. Amoebulae fusing to form plasmodium. All × 540. G. Plasmodium × 90. 1. Nucleus.

bending of the pseudopodia, and when it is brought quite close, a broad irregular pseudopodium, like one of those of *Amoeba*, shoots out and engulfs it. Pseudopodia were defined in the case of *Amoeba* as irregular projections shot out at intervals from the body and soon withdrawn, and the question arises how far we have any right to call by the same name these stiff projections of the Heliozoa. They are, however, true pseudopodia, for if the animal be subjected to strong irritation they are all withdrawn. These animals show a most interesting example of the repetition of parts. The species *Actinophrys sol* and *Actinosphaerium eichhornii* are both

comparatively common inhabitants of our ditches. The first is, however, exceedingly minute, not more than $\frac{1}{1000}$th of an inch in diameter and possesses only a single nucleus, whereas the second is large enough to be just visible to the naked eye, and has about 200 nuclei. There is here repetition of the nuclei, but no division of the protoplasm, whereas in *Polystomella* there is segmentation of the protoplasm, but no corresponding multiplication of the nuclei. If both were to occur simultaneously and to correspond so that the body were to consist of a number of segments of protoplasm, each

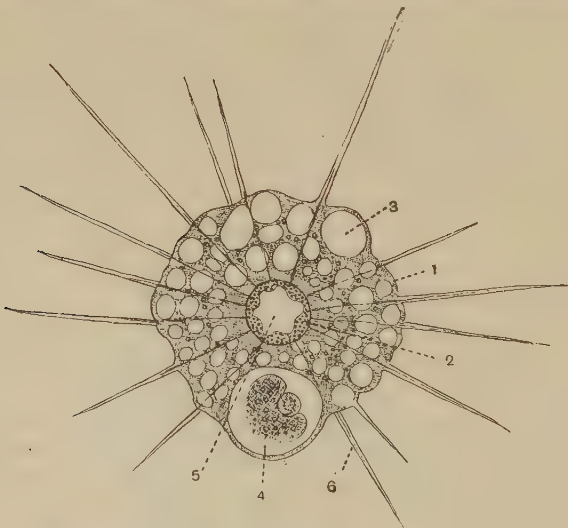

FIG. 8. *Actinophrys sol* × about 800. From Bronn.

1. Ectoplasm. 2. Endoplasm. 3. Contractile vacuole. 4. Food vacuole. 5. Nucleus. 6. Axis of a pseudopodium, stiffer than the protoplasm which covers it.

with its nucleus, the animal would be said to be multicellular, each unit being spoken of as a cell; but it would no longer be a Protozöon.

Actinosphaerium can retract its pseudopodia and encyst itself. The cyst wall contains numerous spicules of silica. This cyst is called the mother-cyst. The nuclei are now rapidly absorbed till only a few of the original 200 remain. The protoplasm then divides into masses each with one of these residual nuclei. These masses secrete round themselves the primary daughter-cysts. The protoplasm inside each daughter cyst divides into two spores which secrete round themselves secondary cysts. The nucleus of each

spore divides twice, but one daughter of each division is absorbed—so that one residual nucleus remains after both divisions. Then the secondary cyst walls break down and the residual nucleus in each spore unites with its fellow forming a zygote which after a time germinates and grows into a new *Actinosphaerium*. Amoebidea, Thalamophora, Radiolaria and Heliozoa on account of their power of emitting pseudopodia are sometimes united in one large division called Rhizopoda.

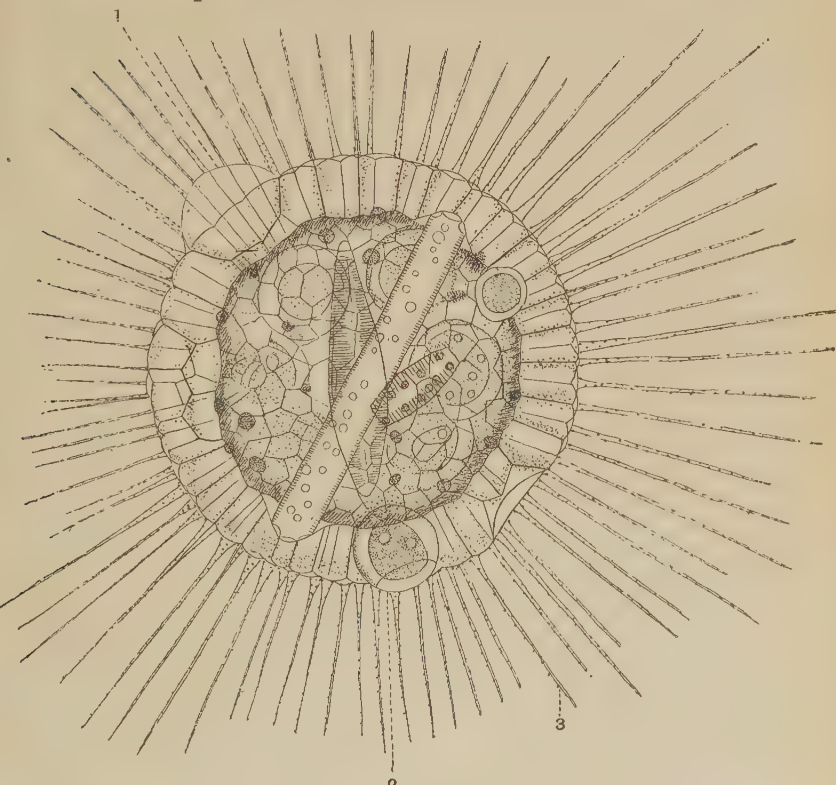

FIG. 9. *Actinosphaerium eichhornii* × 200. From Leidy. The endoplasm is crowded with food vacuoles containing Diatoms, and nuclei are represented in the figure by the dark areas.

1. Contractile vacuole. 2. Food vacuole which has just swallowed a Rotifer. 3. Pseudopodia.

Flagellata.

The next group of the Protozoa we shall consider is a very large and important one. It is called the Flagellata. The members of it are characterised by having one or more flagella, that is whip-like threads, which lash about in the

water, and drag the animal after them by a spiral screw-like motion, just as a steamship is dragged by the screw when the engines are reversed. These flagella as we have already seen are carried by the germs of some Thalamophora, Mycetozoa and Radiolaria, but in the Flagellata they are permanent. In many cases where the matter has been closely investigated each flagellum is seen to originate in a minute basal granule. We may take as a type *Euglena viridis*, one of the numerous inhabitants of ditches. This animal has a narrow elongated shape, pointed at one end, and at the other, which is its front end, it possesses a minute pore, which passes through the outer stiffer layer of protoplasm, and at the bottom of which the soft inner protoplasm is exposed. This is termed the pharynx and it is exceedingly narrow. It has a flagellum which

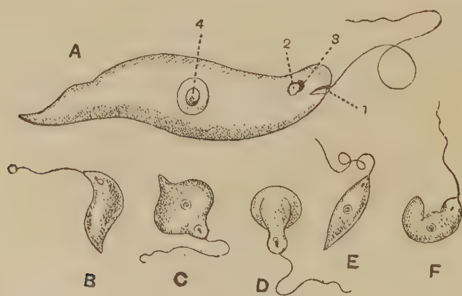

FIG. 10. *Euglena viridis.*

A × 100, B, C, D, E, F × 200 showing the different shapes assumed by the animal during the euglenoid movements. 1. Pharynx. 2. Contractile vacuole. 3. Pigment spot. 4. Nucleus.

arises from its wall near its inner end. Slightly behind the pharynx there is a small clear vacuole, and at the one side of this a small red spot, which may very possibly be associated with a sensitiveness to light. The clear vacuole opens into the pharynx; it is termed the reservoir—for two contractile vacuoles lie behind it and discharge into it. About the middle of the body is a nucleus which can sometimes be made out as a clear spot in the living animal, but which is most satisfactorily observed when the animal is killed with osmic acid and stained with picrocarmine.

Two features in *Euglena*, however, will strike us as very peculiar. One is, that in spite of possessing a permanent cuticle it is able to change its shape. It does not possess the power of throwing out pseudopodia, but it bends its body in the most extraordinary way,

and contracts it till it is almost spherical. The peculiar wriggling movements which it thus executes are so unlike anything else that they have been called euglenoid. The reason for their possibility is that the cuticle is flexible and that the outermost layer of the protoplasm contains differentiated threads termed myonemes which have special powers of contractility. An ectoplasm possessing permanent elements like this is spoken of as a cortical layer. The other peculiarity is still more striking, and it is that the protoplasm is coloured bright green and that it contains particles of a substance very like starch. Now this indicates that *Euglena* feeds itself like a plant, and that it constructs its protoplasm out of carbon dioxide and mineral salts dissolved in water in the presence of sunlight. The only points therefore that can be suggested in which it differs from plants are that it has a flagellum and moves, and that it does not possess a covering of cellulose. These supposed differences, however, will not stand examination; the germs of many undoubted plants, such as, for instance, the sea-weeds, have no cell wall and propel themselves by means of flagella. What justification then, it may be asked, have we for reckoning *Euglena* as an animal? What do we mean by so classing it? It must indeed be admitted that when we come to deal with the simple Flagellata, the animal and plant kingdoms merge into one another, and the only valid line of division we can draw is between forms which feed on solid food, and those which absorb dissolved nutriment; and amongst the latter we call those forms animals which we believe to have been derived from ancestors which fed on solid food. Now the pharynx in *Euglena* takes in solid particles from time to time and these passing into the protoplasm are apparently digested. We might therefore imagine either that *Euglena* is a plant which has acquired a pharynx and is commencing to live like an animal or else that it is an animal that has acquired chlorophyll and has commenced to live like a plant. The fact that the pharynx is small and of little use is against the idea that it is an organ which has been newly acquired—as all organs are acquired—on account of its usefulness. It has the appearance of being the vestige of a once useful organ and therefore we conclude that *Euglena* is an animal which has begun to live like a plant.

The reproduction of *Euglena* and of the Flagellata in general is effected by longitudinal division whilst they are moving about, but they also divide by transverse fission when in an encysted condition into two or four, or a larger number of germs; these germs

are not killed by drought. When dry they are blown about, and so appear in infusions. In infusions Bacteria appear first, then Flagellata, and finally Ciliata (see page 35).

Many Flagellata are devoid of a pharynx altogether, and are without chlorophyll; they subsist on the nutritive substances which are dissolved in the fluid in which putrefying matter is soaking. These are reckoned as animals on no very good grounds; for it is well known that plants can lose their green matter when they can get the materials of protoplasm without building it up from carbon dioxide. How entirely arbitrary the decision is is best shown by the fact that many forms are claimed by both botanists and zoologists. For this reason it is convenient to have a name which denotes simply a living thing without prejudging the question as to whether it is an animal or a plant. Such a name is supplied by the word organism, which is frequently used.

The Flagellata, or Mastigophora as they are sometimes called, exhibit a very wide range of structure and the type described gives a very limited idea of the group as a whole. Many of them are parasitic in other animals and have attracted to themselves a great deal of interest in recent years because it has been proved that they are pathogenic, i.e. causers of disease. A very rapid survey of the principal sub-divisions may be given here. The Rhizomastigina are a curious group of forms intermediate between the Amoebidea and other Flagellata; they are devoid of visible myonemes or a permanent cuticle, but possess the power of emitting pseudopodia. The Silicoflagellata have a single flagellum and possess a spherical perforated shell of silica. Through one aperture of this the single flagellum is protruded. The Dinoflagellata possess a thick cuticle or rather external shell consisting of platelets of cellulose. They possess bodies containing a brown pigment which acts like chlorophyll and live entirely as plants, and on the surface of each there is an antero-posterior and a transverse groove (δῖνος) in each of which a flagellum lies. The largest of these (*Noctiluca*) is just visible to the naked eye. It possesses large vacuoles which enable it to float and thus render locomotor organs unnecessary. The longitudinal flagellum is minute and the transverse one is changed to a short thick tentacle lying in a shortened transverse groove. *Noctiluca*, like most Dinoflagellata, is marine and causes the diffused phosphorescence of the sea, in which it is sometimes present in such numbers as to make the water look like soup. *Noctiluca* is sometimes made the type of a special division termed the Cystoflagellata. The Choanoflagellata possess a

protoplasmic funnel projecting from one end called the collar, from the centre of which a flagellum protrudes. To the collar adhere particles of food swept in by the spiral motion of the flagellum and in its substance they are engulfed. Ordinary Flagellata like *Euglena* are termed Lissoflagellata. The members of this group which live in the blood of animals are often termed Haematoflagellata although this is not a scientific ground of division. Of these the most dreaded is *Trypanosoma*, characterised by having a flagellum bent back at its point of origin and attached to the border of the animal forming the so-called undulating membrane, whilst a free portion projects behind. The nucleus is divided into two, one portion remaining in the centre of the animal whilst another portion, the kineto-nucleus, lies just beneath the flagellum. This animal lives in the blood of vertebrates in one stage of its existence and one species causes in Man sleeping sickness—a disease which is a low fever in its early stages and in its later a disease of the brain. The parasite is conveyed from one person to another by a fly (*Glossina palpalis*) which sucks the blood of the person infected and in this way receives the parasite into its own interior where it undergoes rapid division. The resulting germs are then injected by the fly along with its saliva into the blood of another victim.

Ciliata.

The next group of Protozoa which we shall describe are termed the Ciliata. As the name implies their locomotor organs are numerous cilia which are vibratile hairs like flagella but much shorter and having a simple oar-like motion of a simpler character than the whip-like motion of flagella. The Ciliata differ from all other Protozoa in having two kinds of nuclei, one sort of which only comes into use when the conjugating gametes are formed. If we examine the roots of Duckweed with a lens, we shall probably find some coated with a whitish scum; if these be cut off and mounted in a drop of water on a slide and examined with a low power, they will be seen to be covered by numerous specimens of a most beautiful animal called *Vorticella*. *Vorticella* has something the shape of a blue-bell flower; it consists of a long delicate stalk and a bell-shaped body; by means of the stalk it is fixed to some definite support, such as, for instance, the Duckweed root. The part of the body corresponding to the lip of the bell is broad and turned outwards; encircled by this lip, which is called the peristome, there is a flattened projection called the disc. Between the peristome and disc there is a peristomial groove, and in this we can make out some short hair-like structures waving to

and fro, these are the cilia; there is a circle, or rather one twist of a spiral of these, as we can see when the animal turns the surface of the disc upwards. By the regular rhythmical bending of these cilia, and possibly by the movement of a rolled membrane which projects into the mouth, a vortex is produced in the water, which draws particles of food to the *Vorticella*, as is the case with the higher Flagellata and Sporozoa. The shape of the body, though it varies slightly with the state of expansion or contraction, is practically constant; no pseudopodia are given out. This is the result partly of the possession of a firm membrane covering the whole of the body, called the cuticle, which is a protective secretion like the shell of *Arcella* only much thinner and so intimately connected with the protoplasm under it as to be inseparable from it; but the constancy of shape is also due to the fact that as in Sporozoa or Flagellata the ectoplasm is a cortical layer containing myonemes or fibrils endowed with the power of contraction. The stalk, which is entirely composed of this layer, might almost be regarded as a muscular fibre. The stalk is slightly twisted and attached in a long spiral to the inner side of an elastic tube of cuticle. When contraction occurs the stalk is necessarily thrown into the most evident spiral curves, like a corkscrew; the restoration of the form after contraction is due to the elasticity of the tube of cuticle.

FIG. 11. *Vorticella microstoma* × about 200. From Stein.

Vorticella possesses a contractile vacuole and a nucleus just as *Amoeba* does; in small nearly transparent specimens both are easily detected during life; in fact, if the specimen under observation only keeps moderately still, we can follow the expansion and contraction of the vacuole with the greatest ease. The nucleus is very large and has more or less the shape of a horse-shoe, though the two ends are generally at different levels, so that in reality it forms part of a spiral. If we run in some iodine it at once absorbs the stain and stands out very distinctly; the *Vorticella*, however, frequently shows its dislike to the operation by contracting its body into the shape of a ball and snapping itself off from the stalk: it is then apt to get washed away from its position by the inflowing iodine and we may have to search over the slide to find it. This conspicuous nucleus

is termed the meganucleus; beside it lies a very much smaller one termed the micronucleus (Fig. 12). When a *Vorticella* is irritated, the peristomial lip is turned in so as to lie against the disc, and thus the groove in which the cilia lie becomes converted into a tube and so they are efficiently protected.

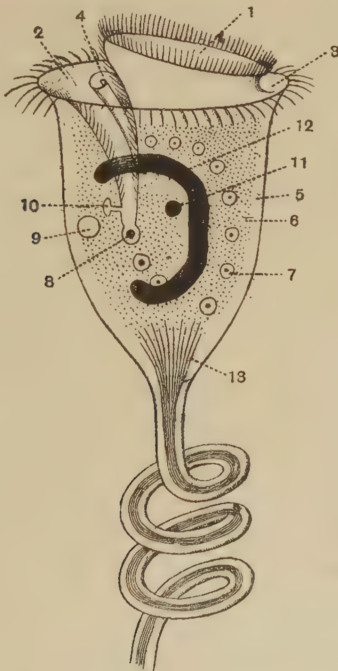

FIG. 12. Diagram of *Vorticella*. The cilia at the side of the mouth have been omitted.

1. Disc. 2. Mouth. 3. Peristomial groove. 4. Vibratile membrane in mouth. 5. Cortical layer. 6. Endoplasm. 7. Food-vacuoles. The last of the food-vacuoles is nearing the position of the anus. 8. Pharynx showing formation of food-vacuoles. 9. Contractile vacuole. 10. Permanent receptacle into which the contractile vacuole opens. 11. Micronucleus. 12. Meganucleus. 13. Contractile fibrils running into muscle in stalk. 14. Stalk contracted (the axial fibre should touch the cuticle in places).

We have seen above that *Vorticella* uses its cilia in order to produce a miniature whirlpool in the water by means of which particles of edible matter—whether living or not—are drawn towards it. Since, however, it possesses a firm cuticle and in addition a specialised outer layer of protoplasm, the question arises how the food is taken into the interior of the body. If we run

some Indian ink under the cover-glass we shall have a demonstration of how this is managed. The black particles are caught in the whirlpool made by the cilia, they course round and round and finally accumulate in a pit which opens into the ciliated groove and from the bottom of this they pass one by one into the internal protoplasm of the body. This pit which obviously passes through both the cuticle and the cortical layer is the pharynx and its opening the mouth. The particles of Indian ink which have passed into the body are surrounded by little drops of fluid which are partly swallowed with it and partly secreted by the protoplasm, in order to effect the solution of the particle, that is, its digestion. Such a drop is called a food-vacuole in order to distinguish it from the contractile vacuole, which, as we have seen (page 17), has probably an excretory office to perform. As there is nothing nutritious in Indian ink, the *Vorticella* soon gets tired of trying to digest it, and the particles after having travelled through the body in a more or less definite tract are thrust out into the ciliated groove. Since this takes place at only one spot, there must be a permanent hole in the cuticle here though we cannot discern it, and this opening may be called the anus. Therefore in contradistinction to *Amoeba*, where food can be taken in and undigested remnants cast out at any spot on the surface, in *Vorticella* it is only at one particular spot that either action can take place.

The reproduction of *Vorticella* is a most interesting process. It takes place by longitudinal splitting, or, as it is technically called, fission. The disc splits into two, and the cleft soon reaches right down to the beginning of the stalk, so that for a time we have two bodies attached to the same stalk. One of these acquires a new row of cilia round its base; soon after the original circle of cilia and the peristomial groove disappear; the animal then breaks loose from the stalk and swimming by means of its new circle of cilia seeks a new place of rest. The other body remains on the original stalk and resumes its ordinary life.

Like *Amoeba*, *Vorticella* encysts and it appears still more frequently than *Amoeba* in infusions. The *Vorticellae* which are found under these circumstances are usually small and transparent and more favourable for observation than those occurring in ditches. The genus occurs both in fresh and salt water.

The class Ciliata is a large one and we may now describe another member of it which is frequently found in infusions of decaying animal and vegetable matter. This animal is termed

Paramecium, it appears after the Flagellata (see p. 31) on which it appears to feed. It is often termed the Slipper animalcule because it is of an elongated oval outline and seen sideways it has a thin scoop-like anterior end and a thick posterior part, so that it is usually described as slipper-shaped. It is covered all over with cilia of the same size arranged in regular lines; this arrangement of cilia, which is called the holotrichous arrangement (ὅλος, entire; θρίξ, hair), is always associated with the absence of a stalk and with a free-swimming life. *Vorticella*, on the other hand, is said to be peritrichous (περί = around). *Paramecium* like *Vorticella* possesses two nuclei, one large and easily visible and one, the micronucleus, small and difficult to detect. It has a well-developed mouth and a deep pharynx situated on one side and lined with specially long cilia. *Paramecium* is a beautiful form in which to study the contractile vacuole; there are two of these present, one in the anterior and another in the posterior portion of the animal. If one of these vacuoles be watched it can be seen to contract and then slowly to re-appear. In the process of re-appearance six radiating channels are seen through which the liquid streams so as to form a perfectly spherical drop. These seem to be permanent channels in the protoplasm leading to a central space which becomes filled with fluid and and forms the vacuole.

Paramecium possesses peculiar organs named trichocysts (5, Fig. 13) embedded in the outer layer of the protoplasm. These look like minute rods. When the *Paramecium* is irritated—as for instance if it is deluged with dilute iodine—these are suddenly shot out, assuming the form of long threads, and they are thought to exercise a stunning effect on any small animal with which they come in contact, though no good evidence for this has been adduced.

Prof. Jennings has carefully studied the behaviour of *Paramecium*. Although to the casual eye its movements appear to be guided by intelligence yet all its actions may be reduced to variation in the intensity of one reaction. According to Jennings, when *Paramecium* is not irritated its normal condition is one of actively swimming forwards. When irritated it stops and the anterior cilia become motionless, then the beat of all the cilia is reversed and the animal is thus forced backwards. After retreating for a short space it turns round an axis running from right to left through the middle of the body, the front end bending downwards through a moderate angle. The reaction is now at an end and the normal

state of swimming forward is resumed. If into a film of water full of active *Paramecia* a drop of dilute solution of sugar is introduced the animals pay no attention to it, but soon by chance one traverses it. When it tries to pass out of the drop on the other side it is stimulated and its one reaction called forth. As a consequence it is forced back into the centre of the drop, and the reaction is

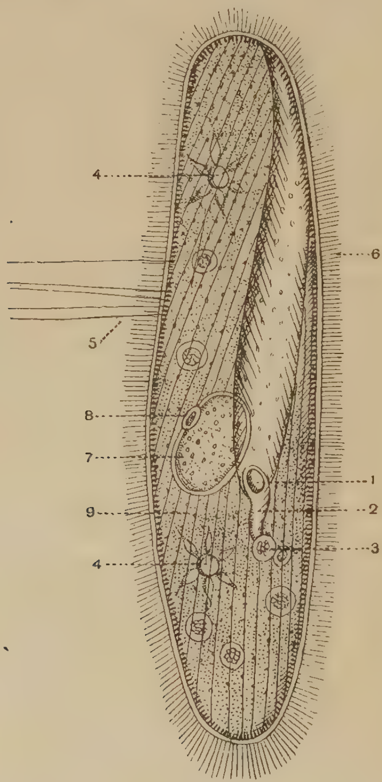

FIG. 13. *Paramecium caudatum* × about 250. After Bütschli.
1. Mouth at bottom of groove. 2. Oesophagus. 3. Food vacuole just being formed. 4. Contractile vacuoles. 5. Trichocysts which have exploded: the unexploded ones line the cuticle. 6. Cilia. 7. Meganucleus. 8. Micronucleus. 9. Contractile fibrils.

repeated every time the animal approaches the edge, so that the *Paramecium* remains a prisoner. Soon another is caught and after a time the drop is crowded. They can only be released when the sugar is all finally assimilated by them. If on the other hand the drop consists of moderately strong acid then the reaction is called

forth when a specimen first touches the drop—it is forced back and turned to one side and when it resumes its normal state it will probably pass by the side of the obstacle. Thus the behaviour of *Paramecium* is almost as simple as that of a Jack-in-the-box. Other Ciliata such as *Vorticella* are a little more complex in their behaviour; they may have two or even three reactions, but in none is there any question of intelligence.

If a single *Paramecium* be introduced into a sterile food solution it will grow and rapidly multiply, and if when the solution is used up a single individual of the brood be transferred to another solution the race may be kept going through hundreds of generations. Such a race all sprung from a single individual is termed a pure culture. After some hundreds of generations the members of a pure race attempt to conjugate with one another, but nothing results. Soon after they exhibit signs of degeneration, imperfect individuals without mouths result from fission and the whole race perishes in the midst of plenty of food. This catastrophe can be staved off by adding stimulating substances to the solution (Calkins) but cannot be finally averted. If however members of a different culture are introduced successful conjugation takes place and the vitality of the culture is renewed. When such a conjugation is about to take place two individuals approach and place their oral surfaces in contact, the mouths and gullets of both disappear and their protoplasm fuses. The meganucleus breaks up into pieces which are absorbed. The micronucleus in each divides into eight nuclei and of these seven are absorbed the remaining piece divides into two and one of these migrates into the other animal and fuses with the resting half of its micronucleus forming thus a zygote nucleus. Thus it may be said that each animal gives off a single male gamete to the other and is itself the female gamete. The animals then separate and each forms a new mouth and pharynx. The zygote nucleus then divides into eight nuclei, four of which enlarge to form new meganuclei. Then the animal divides into two, each daughter having two micronuclei and two meganuclei; then after a day or two it divides again and now the cycle is complete, each daughter having one meganucleus and one micronucleus. The whole process of conjugation has for its result the installation of a new meganucleus and the idea is suggested to the mind that in the processes of ordinary division and growth during which the meganucleus must be giving off substances into the protoplasm, it becomes worn out in its essential parts and must be replaced, and this can only happen if nuclear matter from another source, which if worn out is probably

not worn out in the same manner, is received. The micronucleus and meganucleus are sisters and the micronucleus corresponds to the "chromidium" of the Rhizopoda which is given off from the primary nucleus and which gives rise to the gametes. The fact that it divides into eight pieces of which only one survives probably points back to an ancestral condition in which numerous gametes were found. *Vorticella* conjugates in a similar manner to *Paramecium*, but one of the conjugants is a small motile person, the other a large ordinary fixed one. The small partner never frees himself and after delivering the male gamete and receiving another male gamete from the larger partner, he degenerates and is absorbed as food by the larger fixed one so that in every conjugation one individual disappears.

Opalina. found in the intestine of the Frog, is a most aberrant Ciliate and stands in remote relationship to the rest; it is holotrichous like *Paramecium*. This animal is thin and plate-like. *Opalina* is further remarkable for possessing a large number of nuclei (1, Fig. 14), which is a rare occurrence amongst the Ciliata. When, however, division commences it continues until the resulting pieces have only one nucleus each; they then grow and do not divide again till they acquire the size they had before division took place and also the same number of nuclei. Hence we might regard the multiplication of the nuclei as the real reproduction of this form, the division of the protoplasmic body being of lesser importance and setting in later. When the Frog lays its eggs in spring the nuclei of the adult *Opalina* discharge chromatin granules into the protoplasm forming chromidia which aggregate as small dense secondary nuclei; the original nuclei remain as pale spheres for some considerable time. This ejection of chromidia corresponds to the breaking up of the micronucleus in other Ciliata. Division then takes place until the daughters have only four nuclei each. They then encyst themselves, the cysts are discharged into the water and if swallowed by a tadpole burst, giving vent to four ciliated gametes each with one nucleus, which then conjugate with one another.

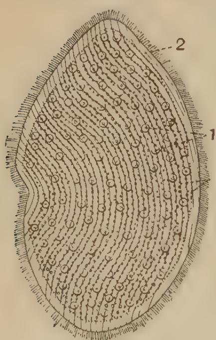

FIG. 14. *Opalina ranarum*. Highly magnified. From Bronn.
1. Nuclei. 2. Ectoplasm.

Passing from the Ciliata, we next come to a small group called the

Suctoria.

Suctoria, which are allied to the Ciliata, for their buds commence life as small ciliated forms. When they

grow up they frequently become stalked like *Vorticella*, but they lose their cilia and acquire instead a number of stiff rod-like outgrowths ending in knobs; these structures are termed tentacles. These are able in some way which we do not understand to seize small animals and suck out their contents. Some secretion must be produced which eats its way through the cuticle and dissolves the contents of the prey. Suctoria have micronuclei and conjugate like Ciliata.

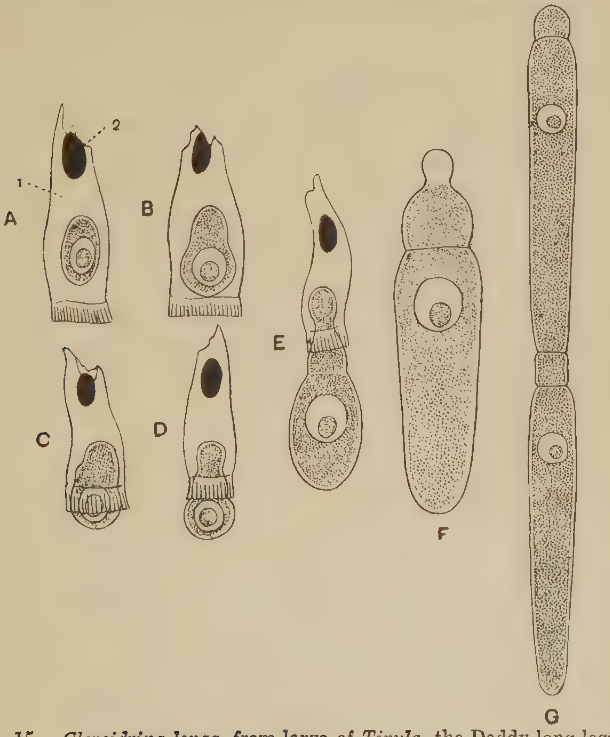

FIG. 15. *Clepsidrina longa*, from larva of *Tipula*, the Daddy-long-legs. Highly magnified. From Léger.

A, B, C, D, E. Stages of the development of *C. longa*, at first within and then pushing its way out of one of the cells of the intestine of the *Tipula* larva. F. Mature form. G. Two forms conjugating. 1. Cell of intestine of host. 2. Its nucleus.

Sporozoa.

The last group of Protozoa, the Sporozoa, agree with the Flagellata in showing a great range of forms, the lowest of which can emit pseudopodia whilst the more highly specialised possess a well developed cortical layer with myonemes. None possess cilia or flagella; their movements, which are very sluggish, are carried out entirely by contractions of the cortex, which give rise to worm-like wrigglings. The name,

Sporozoa, suggested by the frequently recurring formation of spores, which is a marked feature in the life-history, is inappropriate, as we have seen reason to believe that something analogous occurs in all Protozoa; but it is characteristic of Sporozoa that the contents of each spore break up into a number of amoeboid young. All the Sporozoa are parasitic; that is to say all live at the expense of some other animal which is termed the host. All as a matter of fact pass the first period of their existence embedded in the protoplasm of some animal. Some—the Coccidea—remain throughout life in this position, but others when fully grown become at any rate partly free, adhering to their hosts only by one end. Only fluid nourishment is absorbed and consequently there is neither mouth nor anus. The Sporozoa are thus contrasted with the Haematoflagellata which appear to pass all stages of their existence in the fluids of their host. There is usually one nucleus, although the body may be divided into two or even three portions by partitions running across the protoplasm placed one behind the other. Reproduction takes place by fission and by the production of naked germs which conjugate called gametes. The resulting zygote secretes a cyst wall and forms the spore. The contents of this spore break up into several so-called "falciform embryos" which are really amoeboid young.

Among the better known Sporozoa are *Monocystis* found in the vesicula seminalis of the Earthworm, with a long worm-like undivided body, *Clepsidrina blattarum* found in the intestine of the Cockroach and *C. longa* in the intestine of the larval grub of the Daddy-long-legs, which lives in damp soil. This last form is quite free when adult and is distinctly divided into two portions.

In recent years it has been discovered that many of the Sporozoa, like the Haematoflagellata, cause disease, and a great amount of study has been devoted to this group. Leaving out of consideration the little known Neosporidia in which fission and the formation of spores go on at the same time, the more normal Sporozoa are divided into three groups, viz. Gregarinidea, Coccidea and Haemosporidia. To the first named belong the two forms just mentioned. In this family two fully adult individuals termed trophozoites approach one another and become surrounded by a common cyst wall, termed the sporangium. Within this both break up into gametes, and the naked oval gametes conjugate in pairs. The zygotes then surround themselves with boat-shaped flinty cases and become the spores, or "pseudonavicellae," the contents of each of which breaks up into

usually eight falciform young. All the Gregarinidea in the adult stage are at least partly free from the cells of the host. The Coccidea consist of forms in which the trophozoite remains completely immersed in the cells of the host. The adults divide into sickle-shaped young which escape and enter other cells; after a time they become converted into male and female forms, the so-called microgametocytes and megagametocytes. In the former the nucleus breaks up into minute rod-like portions which acquire flagella and become free in the alimentary canal of the host. The megagametocyte rounds itself off and forms the female gamete, drops out of the cell in which it is, into the alimentary canal and is here fertilised. The zygote develops into a sporangium, the contents of which divide into several spores and each spore gives rise to several amoeboid young.

The Haemosporidia differ from the two foregoing familes in the following points.

(1) The adult inhabits the cells of the blood of the host, not of its alimentary canal.

(2) The adult has its cortical layer badly or not at all developed, so that it resembles *Amoeba* in its power of changing its shape. The Haemosporidia agree with the Coccidea in possessing gametes of two sizes, but the sexual phase is usually passed in the interior of an insect, whilst the stage of asexual multiplication is passed in the blood of a Vertebrate. *Laverania malariae* is the cause of ague or malarial fever. The adult lives in a red blood corpuscle (see p. 433) and eats it out, transforming the red haemoglobin into black pigment (melanin). The parasite then divides into sickle-shaped young (as in the Coccidea) which escape into the blood and cause an onset of fever. They soon enter and attack other blood-cells. If the blood of a patient is sucked by the mosquito *Anopheles*, the parasite becomes changed into the sexual form in the stomach of the insect. As in Coccidea megagametocytes and microgametocytes are formed, and the small male gametes fertilise the large rounded female gametes. The zygotes force their way through the wall of the insect's stomach into its blood, and there become surrounded with a cyst wall. The contents divide into sickle-shaped young and these migrate into the salivary glands of the Mosquito and await their opportunity of entering the wound which the Mosquito makes on the next person it bites. *Piroplasma* is a similar parasite in the blood of cattle where it causes red-water fever. It is transmitted from one beast to another by a tick.

Phylum PROTOZOA.

The Protozoa are classified as follows:

Class I. Rhizopoda.

Protozoa devoid of a cuticle and capable of emitting pseudopodia.

Order 1. **Amoebidea.**

Naked forms devoid of a shell.

Order 2. **Thalamophora.**

Rhizopoda which secrete a shell protecting at least part of the surface of the body. Ex. *Arcella*, *Difflugia*, *Gromia*, *Polystomella*.

Order 3. **Radiolaria.**

Rhizopoda with an internal capsule, i.e. a membranous shell protecting the inner part of the body. Outside this a lattice-like shell of flinty needles. The pseudopodia are delicate filamentous and interlacing. Ex. *Heliosphaera*.

Order 4. **Heliozoa.**

Rhizopoda with stiff radiating pseudopodia. A lattice-like shell present or absent. Ex. *Actinosphaerium*, *Actinophrys*.

Order 5. **Mycetozoa.**

Rhizopoda of large size with numerous nuclei and with coarse branching pseudopodia which form networks; they form spores with cellulose walls.

Sub-order 1. **Endosporeae.**

Spores formed inside a sporangium

Sub-order 2. **Exosporeae.**

Spores constricted from finger-like processes

Class II. Flagellata.

Protozoa provided with one or several flagella. When two nuclei are present one is situated near the base of the flagellum and is related to its activity.

Order 1. **Rhizomastigina.**

Forms capable of emitting pseudopodia.

Order 2. **Silicoflagellata.**

Forms with one flagellum and a latticed siliceous shell.

Order 3. **Dinoflagellata.**

Forms with a thick cellulose cuticle and with transverse and longitudinal grooves each containing a flagellum.

Order 4. **Choanoflagellata.**

Forms with a protoplasmic collar surrounding the base of the flagellum.

Order 5. **Lissoflagellata.**

Forms with well-marked cuticle and myonemes but no collar, skeleton, or groove. Lissoflagellata parasitic in the blood are termed Haematoflagellata.

Class III. Ciliata.

Protozoa bearing numerous cilia, at least when young. Vegetative and special sexual nuclei develop.

Order 1. **Holotricha.**

Cilia all over body, all same size.

Ex. *Paramecium.*

Order 2. **Peritricha.**

A wreath of cilia round one end.

Ex. *Vorticella.*

Order 3. **Suctoria.**

Cilia replaced in adult condition by suctorial tentacles.

Ex. *Acineta.*

Class IV. Sporozoa.

Protozoa, with or without stiff cuticle and myonemes, in which spores are formed, the contents of which break up into several amoeboid young. All when young are parasites within the protoplasm of their hosts.

Sub-class I. Neosporidia.

Fission and the formation of spores occur at the same time in different parts of the body.

Sub-class II. Telosporidia.

Fission and formation of spores confined to different periods of the life history.

Order 1. **Gregarinidea.**

Forms which when adult emerge from protoplasm of their hosts and lie free in their internal cavities. Gametes of same size. The zygote forms only one spore.

Ex. *Monocystis, Clepsidrina.*

Order 2. **Coccidea.**

Forms which when adult remain within protoplasm of their hosts. Gametes of different sizes. The zygote forms several spores.

Order 3. **Haemosporidia.**

Forms inhabiting blood-cells of their hosts. Gametes of two sizes.

Ex. *Laverania.*

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CHAPTER III

PHYLUM COELENTERATA

It is difficult to say what idea the originator of the name Coelenterata meant to convey. Most animals have hollow insides (Gr. κοῖλος, hollow; ἔντερον, inside); the Coelenterata however are distinguished from all the more highly organised groups in the animal kingdom by containing inside only one set of spaces, which all communicate with each other and with the exterior through the mouth.

Hydra.

The Coelenterate of simplest structure is undoubtedly the common fresh-water Polyp (*Hydra*) (Fig. 16). If a mass of weed and other débris from a ditch or even the edge of a river be placed in a glass vessel along with some of the water in which it was grown, and allowed to settle, a number of these small animals frequently termed polyps will usually be found collected on the side of the vessel nearest the light. Several distinct species are collected under the name *Hydra*. There are three species recognised in Great Britain; *Hydra fusca*, about a third of an inch long when expanded and of a whitish yellow colour, *Hydra viridis*, a quarter of an inch long, of a green colour, and *Hydra vulgaris*, which is almost colourless. Similar species to the first two, if indeed they are not identical, are common in Lower Canada. *Hydra fusca* may be selected as a type.

The shape of this animal is that of a minute cylinder. The base or foot is attached to the surface of the glass by an adhesive disc, whilst the other extremity carries a circle of delicate thread-like appendages called tentacles. In the centre of these, near their point of origin, we can with a lens detect a minute conical elevation, the oral cone (2, Fig. 16), at the end of which is the mouth. The mouth is the only opening in the body and it leads into a space which occupies the whole extent of the animal, so that we might

with justice say that the polyp is really simply a tube closed at one end and open at the other: further, the tentacles can be seen with the microscope to be nothing but thin hollow tubes, opening into the central one (Fig. 17). The central space is often termed a stomach, and in the case of *Hydra* the idea suggested by this

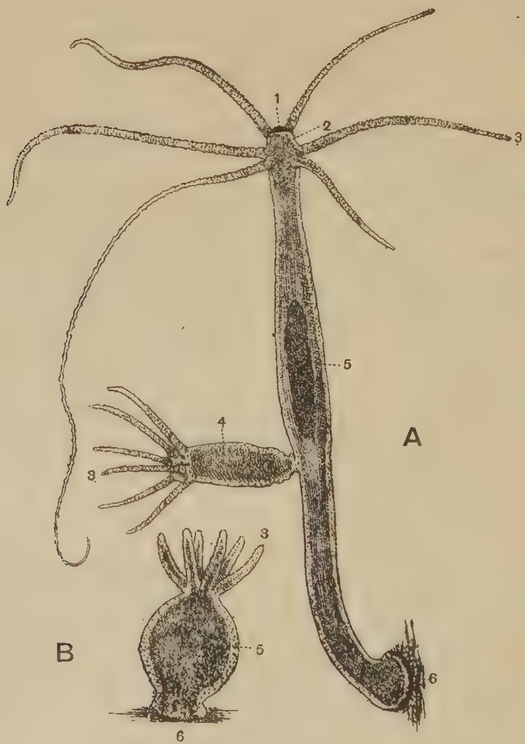


FIG. 16. *Hydra fusca* × about 12.

A. Expanded condition. This specimen is budding off a young *Hydra*. It contains a large food mass in its coelenteron, probably a Daphnia or some other fresh-water Crustacean. B. Retracted condition. 1. Mouth. 2. Oral cone. 3. Tentacles. 4. Bud. 5. Endoderm. 6. Foot.

term is correct. In other Coelenterata the space performs other functions besides those of the human stomach, and the term coelenteron, which does not imply any function, is preferable.

With the microscope, however, we can make out a number of further points. If the edge of the animal be carefully focused it can be seen that the body-wall consists of two layers, an outer

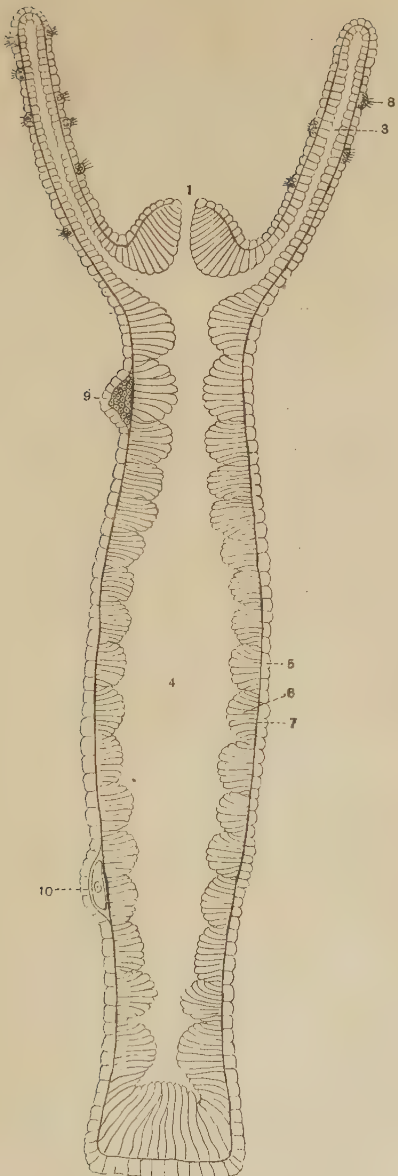


FIG. 17. A longitudinal section through the body of a *Hydra*: somewhat diagrammatic, the details of the cells being omitted. Magnified.

1. Mouth. 2. Foot. 3. Tentacle. 4. Coelenteron or digestive cavity. 5. Ectoderm. 6. Endoderm. 7. Mesogloea or structureless lamella. 8. Batteries of thread cells. 9. Testis. 10. Ovary with single ovum.

clear one, termed the ectoderm (Gr. ἐκτός, external; δέρμα, skin), and an inner one called the endoderm (Gr. ἔνδον, inside), which is green in *Hydra viridis* and brownish in *Hydra fusca*; so that we may speak of a skin as distinct from the lining of the coelenteron (Figs. 17 and 18). It is further possible to make out under the microscope that at any rate the outer layer is not homogeneous, but is composed of separate small pieces. It is necessary, however, to examine thin sections of specimens which have been hardened by being soaked in corrosive sublimate or some similar reagent, before one can really get a good idea of the structure of the "skin" and of the "inner lining" of the polyp. Then it is seen that both are made up of the repetition of similar parts, and that in each of these parts there is a single nucleus. Such a portion of protoplasm, marked off from the surrounding parts by a definite boundary, is called by zoologists a cell. The wall or boundary of the cell probably consists of a thin layer of some secretion, in many cases, if not in most, traversed by bars or sheets of protoplasm connecting the cell with its neighbours. Around this term "cell" many battles have been waged and its indiscriminate use has led to much misconception.

Cell.

It used to be said, for instance, that the Coelenterata were multicellular animals, as opposed to the Protozoa, which were unicellular. Now it has already been pointed out that the centre of the vital processes is the nucleus, which controls the processes going on in the protoplasm, and that in some of the Protozoa, such as *Actinosphaerium* and *Opalina*, this essential organ is repeated several hundred times. But an *Actinosphaerium* or an *Opalina* certainly does not correspond to a so-called cell of *Hydra*, with its single nucleus; the relation between them may rather be defined by saying that, whereas in *Actinosphaerium* the areas of control of the various nuclei are not visibly delimited from each other, in *Hydra*, on the other hand, this delimitation has to some extent taken place, leading to the appearance of cell-structure. But not only are cells to be detected in *Hydra*; the cells are not all of the same kind. Those forming the endoderm are very big and often have great watery vacuoles near their inner ends; they also contain the coloured granules to which the colour of the animal is due. The cells of the ectoderm or outer skin, on the contrary, are much shorter than those of the endoderm and are more or less pear-shaped, the broader end being turned out. Between their narrower bases we find groups of very small round cells

(2, Fig. 18). These so-called interstitial cells are young cells, which partly, no doubt, become developed into ordinary ectoderm cells as the older cells die and drop off, and in certain seasons of the year they increase very much in number at certain spots and form the reproductive organs (9 and 10, Fig. 17). The two kinds of organs, male and female, are borne by the same individual; in the male organ or testis all the cells remain small and become converted into the small spermatozoa; in the female organ or ovary one cell increases very much in size at the expense of the rest and becomes the egg-cell or ovum (10, Fig. 17). There is,

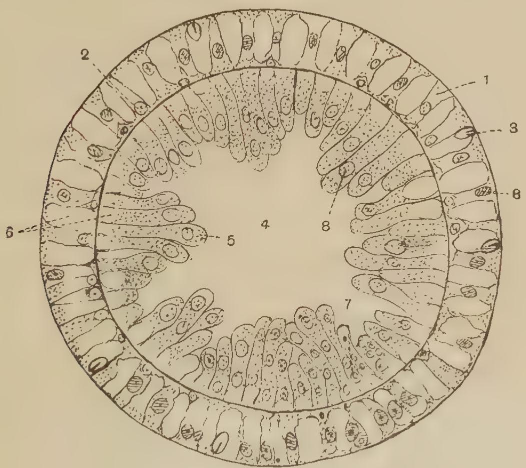


FIG. 18. Transverse section of *Hydra fusca.*

1. Ectoderm cells (myo-epithelial). 2. Interstitial cells. 3. Nematocysts. 4. Coelenteron. 5. Endoderm cells. 6. Vacuoles. 7. Food granules. 8. Nuclei.

however, a third change which these interstitial cells may undergo, which is of the utmost importance to the animal. Some of them move outwards and become wedged between and even embedded in the large ectoderm cells near the surface, each developing in its interior an oval bag filled with fluid. One end of this bag is turned into the interior of it, forming a long hollow thread. The whole bag is called a thread-capsule or nematocyst (Gr. νῆμα, a thread; κύστις, a bladder) (Fig. 19). If now the cell in which the thread-capsule is situated contracts, since the fluid in the capsule is incompressible, the hollow thread must be quickly turned

inside out and thus thrust out of the capsule. If the irritation of skin continues the whole capsule will be pressed out by the animal. These thread-capsules are most abundantly developed in the tentacles, and a small amount of observation of the habits of *Hydra* will show how they are used. If a small Crustacean, or other animal, approaches too near a *Hydra*, the latter makes

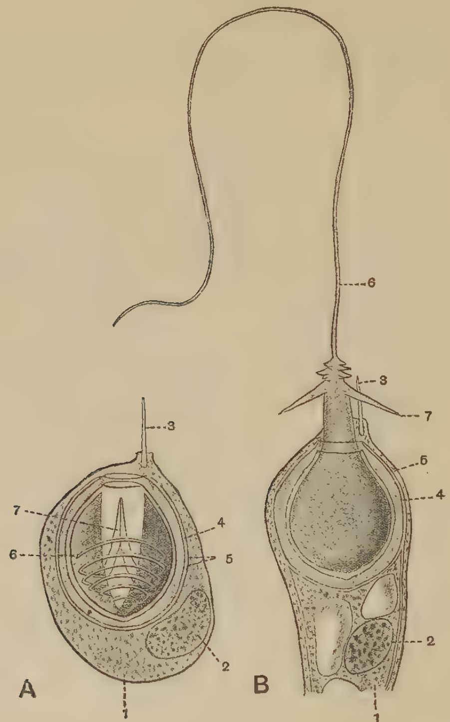


FIG. 19. Cnidoblast with large nematocyst from the body-wall of *Hydra fusca*. Highly magnified. From Schneider.

A. Unexploded. B. Exploded. 1. Cnidoblast. 2. Nucleus of cnidoblast. 3. Cnidocil. 4. Muscular sheath. 5. Wall of nematocyst. 6. Thread. 7. Reflexed processes.

one swift lash with its tentacles and the luckless water-flea is seized and at the same time paralysed. If we now remove and examine the prey, we shall find it covered with exploded thread-capsules, the threads of which have entered its body, and exerted a poisonous action on it. It is possible to induce a *Hydra* which is being observed under the microscope to eject its thread-capsules: we

have only to irrigate it with a little ten per cent. solution of common salt, and from all parts of the skin we shall see first the threads shoot out, and then the capsules follow.

In the case of a fluid like salt solution, the stimulating action is no doubt exerted over the whole surface of the animal, but an examination of the tentacle when it is extended reveals an arrangement for bringing about the explosion of the thread-capsule. The surface of the tentacle is seen to be covered with little swellings, in which are collections—one might say, batteries—of thread-capsules (8, Fig. 17); and from the surface of the ectoderm, in which they are embedded, delicate hair-like rods project out into the water (3, Fig. 19). These rods are called cnidocils (Gr. κνίδη, a nettle; Lat. *cilium*, an eyelash) and are the simplest form of sense-hairs met with in the animal kingdom. If one of these be touched, it transmits a stimulus to the cell containing the thread-capsule, the cnidoblast (Gr. κνίδη, a nettle; βλαστός, a sprout), as it is termed; in response to this stimulus the cell contracts, presses on and explodes the capsule.

In the first chapter it was pointed out that protoplasm, when it effects movements, nearly always does so by contracting. Thus the wrigglings of *Euglena*, the lashings of cilia and flagella, are due to the contractions of myonemes, and even the emission of pseudopodia may be due to a similar cause (p. 17). In the life of *Hydra* the principal movements which occur are the shortening and lengthening of the body and the tentacles (B, Fig. 16). Now it has been found that in these movements, the shortening is effected by the contraction of the ectoderm in a longitudinal direction, and the lengthening by the contraction of the endoderm in a transverse direction, in consequence of which the animal is rendered thinner and longer. It has been further ascertained, by the examination of very carefully prepared longitudinal sections, that each ectoderm cell possesses at its base a tail running vertically, which is embedded in the thin layer of jelly sometimes called the structureless lamella or mesogloea (Gr. μέσος, intermediate; γλοία, glue), which separates ectoderm and endoderm (Fig. 20). The endoderm cells similarly possess short tails, embedded in the jelly, but these run transversely. These tails then are instances of the tendency of protoplasm, which contracts regularly in one direction, to be drawn out into fibres in that direction, or, in other words, we have before us the first step in the conversion of an ordinary cell into a muscle cell. Cells

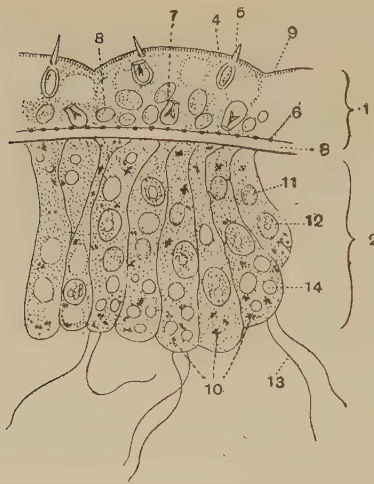


FIG. 20. Section through the body-wall of *Hydra fusca*. Highly magnified. After Schneider.

1. Ectoderm. 2. Endoderm. 3. Mesogloea or structureless lamella. 4. Nematocyst. 5. Cnidocil. 6. Muscle-fibres of ectoderm cells cut across. 7. Nucleus of ectoderm cell. 8. Interstitial cells. 9. Cuticle. 10. Pigment granule. 11. Food granule. 12. Nucleus of endoderm cell. 13. Flagellum. 14. Water vacuole.

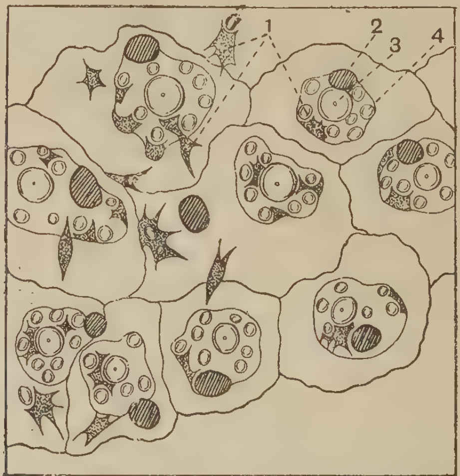


FIG. 21. Preparation of part of the body-wall of *Hydra* to show the nerve-cells. (After Hadzi.) The endoderm cells are omitted.

1. Nerve-cell. 2. Nucleus of ectoderm cell. 3. Large cnidoblast. 4. Small cnidoblast.

showing this modification are termed myo-epithelial (Gr. μῦς = muscle): the word epithelial is used to signify the arrangement of cells in a layer to form a pavement or mosaic.

When a *Hydra* is severely irritated we find that not only the nematocysts but often the cnidoblasts themselves are expelled from the body. This points to the fact that the irritation has spread from the cnidocil to the cnidoblast and thence to the neighbouring ectoderm cells. The question arises how it passes from one cell to another, and this question is raised in a more acute form when we see the whole body of a *Hydra* thrown into contraction as the result of *one* of the tentacles touching a water-flea. The prey is grasped by *all* the tentacles and pushed into the mouth. How are the movements of *Hydra* co-ordinated? Renewed research has within recent years proved the existence of a number of star-shaped cells lying on the jelly at the base of the ectoderm (Fig. 21). Each cell has a central body and a number of radiating processes. The processes of adjacent cells touch each other so that together they form a network (Fig. 22). These cells receive the stimulus from one ectoderm cell and transmit it to others. Their function is to collect, add together and distribute stimuli. They are the most primitive form of n e u r o n s or n e r v e c e l l s and their processes may be looked on as the forerunners of nerve fibres.

Fig. 22. Diagram of *Hydra* to show the arrangement of the nerve-cells. (After Hadzi.)

1. Tentacle. 2. Mouth. 3. Foot. 4. Nerve-cell.

The most important function of the endoderm cells is to digest the prey which is captured by the tentacles and thrust into the coelenteron. For this purpose they secrete a fluid which has a great power of dissolving protoplasm. This fluid, termed d i g e s t i v e j u i c e, is poured forth into the coelenteron and a large portion of the prey is dissolved by it and passes by diffusion into the endoderm cells, from which part is transferred in a similar manner to the ectoderm. Certain portions of the prey, consisting of some of the proteids, resist the action of this juice. These are seized by

pseudopodia emitted by the endoderm cells and bodily engulfed, to be subsequently slowly digested in food vacuoles. Any insoluble parts of the prey, such as cuticle, skeleton, etc., are ejected by the mouth. Some of the endoderm cells also bear flagella, whose movement doubtless aids the circulation of the fluid in the coelenteron.

We have already seen that *Hydra* at certain seasons of the year, viz., the late autumn, produces egg-cells (ova) and male germs (spermatozoa). The latter are shed out into the water, and eventually some of them reach the egg-cells and unite with them. This process is called fertilisation, and the fertilised egg-cells cover themselves with spiny coats and drop off into the mud. Here they remain through the winter; in the spring the hard coat cracks and out issues a minute *Hydra*.

FIG. 23. *Obelia helgolandica* ×1. From Hartlaub. This is the hydroid generation, natural size as it appears to the naked eye.

But *Hydra* is by no means limited to this method of sexual reproduction in its power of multiplying itself. All through the spring and summer, if it be well fed, it buds or reproduces itself by gemmation. A small swelling makes its appearance on the side of the body; this is really a hollow pouch containing a cavity in communication with the coelenteron (4, Fig. 16). The walls of the pouch are merely continuations of the body-wall of the *Hydra*, and hence consist of the same two layers. The pouch rapidly lengthens, and after a while a circle of tentacles sprouts out from its free end, and a mouth is formed in the centre. We thus have a daughter *Hydra* still in close connection with the parent, the coelentera of the two being in open communication; later, however, this communication becomes closed and the offspring separates from the parent and leads a free existence. A third method of reproduction, which probably rarely occurs except artificially, is fission. If a *Hydra* be divided into two halves, each half will grow up into a new individual.

Hydro-medusae.

A large number of the Coelenterata, called the Hydromedusae, agree with *Hydra* in all essential points of structure; the most important point of difference is that in them the buds do not become separated, but remain permanently in connection with the parent, and thus complicated colonies are built up (Fig. 23). Other differences of less

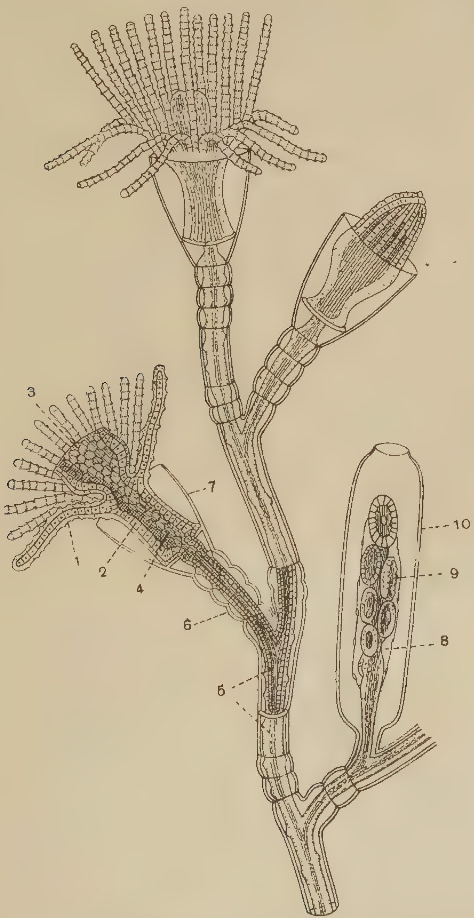


FIG. 24. Part of a branch of *Obelia* sp. To the left a portion is shown in section. After Parker and Haswell.

1. Ectoderm. 2. Endoderm. 3. Mouth. 4. Coelenteron. 5. Coenosarc. 6. Perisarc. 7. Hydrotheca, prolonged at base of hydroid as a shelf. 8. Blastostyle, a mouthless hydroid bearing medusa-buds. 9. Medusa-bud. 10. Gonotheca, part of perisarc which protects the medusa-buds.

importance are that there is a horny shell, the perisarc (Gr. περί, around; σάρξ, flesh) (Fig. 24), secreted by the ectoderm at any rate on the lower portion of the body, also that the tentacles are nearly always solid, containing, instead of tubular outgrowths of the endoderm, a solid cord of cells (Fig. 24) with firm outer membranes and partially fluid contents, so that the cells have the same kind of stiffness as a well-filled water-pillow. These cords likewise grow out from the endoderm, but, as apparently the animal does not need the tentacle cavity which exists in the *Hydra*, it has disappeared, and the solid axis is essentially a strengthening or skeletal structure. As in *Hydra*, there is an oral cone; and in some species of Hydromedusae, at any rate, there is an additional row of short tentacles at the tip of this. It has been stated above that the buds do not become detached, but there is one kind of bud differing much in shape from the rest which does become detached. In

Medusa.

such a bud, the whole body becomes very much shorter and at the same time much flattened out in its lower portion, so that the main circle of tentacles is widely separated from the oral cone; at the apex of the latter there is sometimes a second circle of small tentacles. The bases of the longer tentacles which spring from the flattened part of the body are connected together by a web of skin, which constitutes in this way an umbrella or bell. The endodermal canals of the tentacles within this web are termed radial canals. The radial canals are at first quite separate from one another, but they soon acquire broad fringes of endoderm at their sides, and these unite with those of adjacent canals so as to form a continuous sheet of endoderm, the endoderm lamella. The radial canal branches within this lamella and some branches meet those of adjacent canals and form a circular or marginal canal. Other branches lead into extra tentacles so that in *Obelia* there may be a large number of tentacles at the edge of the umbrella although there are only four radial canals. In other species the young bud has the same number of tentacles as

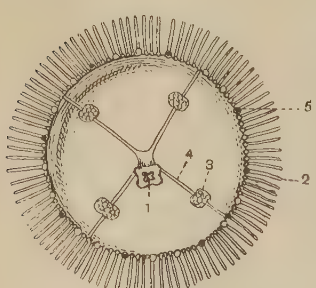


FIG. 25. Free-swimming Medusa of *Obelia* sp.

1. Mouth at end of manubrium.
2. Tentacles.
3. Reproductive organs.
4. Radial canals.
5. Auditory organ.

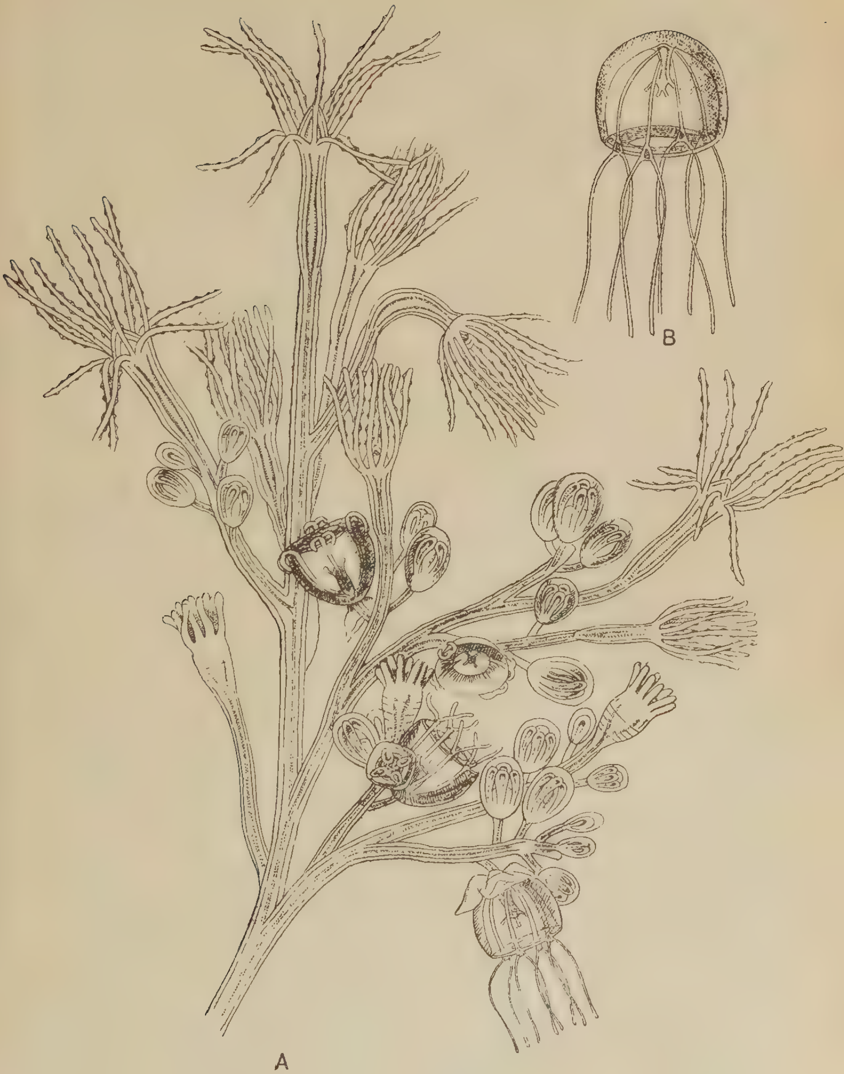


Fig. 26. *Bougainvillia fructuosa*, × about 12. From Allman.

A. The fixed hydroid form with numerous hydroid polyps and medusae in various stages of development. B. The free-swimming sexual Medusa which has broken away from A.

there are radial canals, but as it grows the primary tentacles branch and become bunches of tentacles. The upper surface of the bell is styled the exumbrella or aboral surface (Lat. *ab*, away from; *os, oris*, the mouth), the lower the subumbrella or oral surface.

The great mass of the bell is composed of the jelly intervening between the outer ectoderm on the convex side and the endoderm. In this jelly solid strings sometimes appear which give it a firmer consistence. The union of certain of the tentacles by means of a web so as to simulate an umbrella causes the oral cone to resemble the handle, hence the name manubrium (Lat. a handle), by which it is usually designated in a bud of this kind (1, Fig. 25). Just above the circular canal in most Medusae a fold of the outer skin grows in towards the oral cone, so as to form a broad circular shelf: this structure is called the velum (Lat. an awning) (B, Fig. 26; 1, Fig. 27, II). The bud now breaks loose and swims by contractions of the bell, aided by vibrations of the velum. Anyone would now recognise it as a minute jelly-fish, though it really is quite different in many points from the larger and better known animals denoted by that term. Zoologists speak of it as a Medusa, and speak of the stock from which it was budded as a colony consisting of medusoid and hydroid persons, the latter term denoting the ordinary buds which resemble *Hydra*. The term polyp is an unfortunate one. It really refers to the swollen end piece of a hydroid person carrying the mouth and tentacles. The early naturalists supposed this to be something distinct from the lower stalk-like portion of the body which they called the "coenosarc." A medusoid is in many respects more highly developed than the hydroid person. The ectoderm cells composing the velum and those forming the lining of the under side of the bell or sub-umbrella are strongly drawn out into processes which are muscular. In the velum these are arranged so as to form two bands running round the edge of the bell or umbrella, one band being in connection with the upper and another with the lower layer of cells composing the fold of ectoderm of which the velum consists. Just, however, where the velum is attached to the bell, its cells—upper and lower—undergo another and more interesting modification (4 and 5, Fig. 27, II). At their bases a tangle of delicate threads of almost inconceivable fineness appear; these threads are outgrowths of the cells, but far more delicate than those which already in *Hydra* we recognised as the forerunners of muscles; the threads we are now considering are, in fact, nervous in nature, and the tangles of them connected with

the upper and lower layers, respectively, of the velum, constitute an upper and a lower nerve ring. Each thread is to be regarded as the tail of an excessively small ectoderm cell. This nervous system differs from the nerve cells which were described in *Hydra* in that the processes of the cells are longer and finer in proportion to the size of the body of the cell and that the cells are more numerous and that their processes run more or less parallel to one another. Certain of the nerve cells have their bodies still wedged in between neighbouring ectoderm cells: in this case the nerve process issues from the base of the cell and the cell is termed a sense cell.

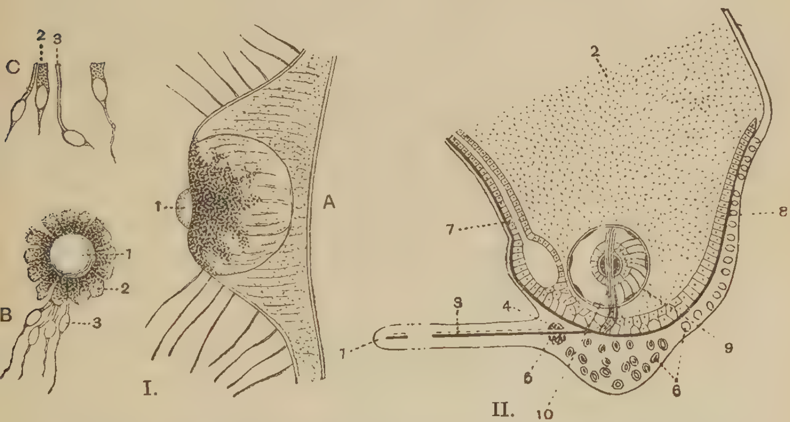


FIG. 27. I. A. Eye of *Lizzia koellikeri* seen from the side, magnified. B. The same seen from in front. C. Isolated cells of the same. From O. & R. Hertwig.

1. Lens. 2. Pigment cells. 3. Percipient cells.

II. Radial section through the edge of the umbrella of *Carmarina hastata* showing sense organ and velum.

1. Velum. 2. Jelly. 3. Circular muscles of velum. 4. Upper nerve ring. 5. Lower nerve ring. 6. Nematocysts. 7. Radial vessel running into circular vessel, both lined by endoderm. 8. Continuation of endoderm along aboral surface. 9. Sense organ or tentaculocyst. 10. Auditory nerve.

In *Hydra* we found the earliest appearance of sense hairs; and the cells of which they are processes, viz., the cnidoblasts, may be called sense cells, although they possess no nerve processes or fibres. In the Medusa we meet with definite collections of sense cells aggregated so as to form sense organs. These are found close to the position of the nerve ring, either on the velum itself or immediately outside it at the bases of the tentacles, so that the stimuli which they receive are easily transmitted to the nerve ring. Two

main kinds of sense organs are frequently found, which may be roughly called eyes and ears; never, however, both kinds in one Medusa. The "eyes" are little coloured patches of skin, some of the cells of which end in clear rods, while others secrete a coloured substance or pigment. Both pigment and rods are necessary if there is to be a vision, though we do not understand why. The ears are little pits in the base of the velum; they may be open or their edges may come together, so that the ectoderm lining them is entirely shut off from the outer skin. In either case, some of the cells forming the walls of the pits secrete particles of lime, others close to them develop delicate sense hairs. The result is that vibrations in the water, if they come with a certain frequency, will affect the heavy particles, and their vibrations in turn will affect the sense hairs. There is another kind of information, however, which organs like these give their possessor, and this is probably still more important to the floating Medusa, namely, information as to the position of the animal with regard to the vertical. In other words, the Medusa learns from them whether it is moving upwards or downwards or sideways: for when the animal shifts its position, the heavy particles in the ear-sacs are shifted comfortably and affect different sense cells.

It is a very interesting fact that "Eyed" Medusae or Anthomedusae arise from hydroid stocks in which the perisarc is confined to the base and in which the first or mother person is taller than the daughters which sprout from her. Such forms are called Gymnoblastea. "Eared" Medusae or Leptomedusae arise from stocks in which the mouth and tentacles are covered by a cup of perisarc called the "hydrotheca" and in which the stem is built up by a daughter sprouting from the mother hydroid's neck and a grand-daughter from the daughter's neck and such forms are called Calyptoblastea. Graptolites or "Pen-stones" from the Ordovician slates of Cumberland are extinct Calyptoblastea.

Through these different sense organs stimuli are continually pouring in from the external world. If the stimuli only affected the contractile cells nearest them irregular movements would result. The function of the nerve ring, as of all nervous systems, is to co-ordinate the stimuli, that is to collect and rearrange and rapidly distribute them to the whole animal so that a definite reaction of the whole contractile tissue results, not a series of local reactions interfering with one another.

The Medusa is very voracious and rapidly increases in size. It

feeds on the small organisms of all kinds, both plants and animals, which are found at the surface of the sea. After some time it commences to give rise either to eggs or to spermatozoa, which usually develop in exactly the same way in which they developed in *Hydra*, i.e., from the interstitial cells of the ectoderm. The accumulations of these cells, called gonads or generative organs, are borne either on the under side of the bell (3, Fig. 25), or on the sides of the manubrium, and it is a curious fact that those Medusae which have them in the former position usually possess ear-sacs, whereas when the gonad is situated on the oral cone, ear-sacs are never present, but eyes may be. The eggs and spermatozoa are both shed out into the water and coalesce there, and the fertilised egg develops

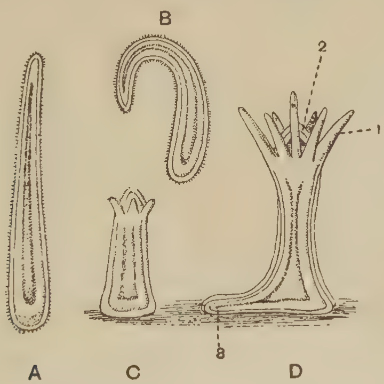


Fig. 28. The ciliated larva or Planula of a Hydromedusan, *Clava Squamata*. Magnified. From Allman.

A & B. Swimming about in the sea. C. Coming to rest on a rock. D. Developing tentacles, oral cone and stolon. 1. Tentacles. 2. Oral cone. 3. Stolon.

into a little oval larva, termed a Planula (Fig. 28), without tentacles or mouth, and covered all over with cilia. It consists at first of a hollow vesicle of ectoderm cells, which later becomes filled with a solid plug of endoderm. This little creature swims about for a while and then attaches itself by one end to a stone or a piece of sea-weed. The attached end flattens out (C and D, Fig. 28), but the rest of the animal lengthens and a mouth and tentacles appear at the free end and the endoderm becomes hollowed out, so that the creature takes the form of an unmistakable hydra-like organism. It then begins to bud out a branch called a stolon which creeps along the substratum. From this other polyps will arise, each of which has only to bud in order to reproduce the colonial stock from which

its parent, the Medusa, was separated. The free-swimming young or planulae furnish good examples of what is meant by the term larva. This name is given to the young form of any animal when it is very different to the fully-grown animal and leads a free life.

Alternation of Generations.

We have thus learnt that a Medusa gives rise to an egg which develops into a Hydroid person, which after a time in turn buds off a Medusa; such an alternation of generations is very characteristic of a large number of Coelenterata. The Medusa represents a sexual generation, the Hydroid an asexual generation, and inasmuch as the Medusoid is often only produced as a bud of the third or fourth order (i.e. is budded from a hydroid person which was produced similarly from another Hydroid person), it will be seen that several asexual generations intervene between two sexual ones. One explanation of this life-history is that the Medusa is only a specially modified Hydroid, which has acquired the power of locomotion in order to disperse the eggs over a large area, and thus avoid the overcrowding of a limited area with one species. The swimming bell and velum are contrivances to enable the bud which bears the eggs to move about. If, however, this explanation be adopted, it is a most remarkable fact that in many species the Medusae are very imperfectly developed and never become free. Such Medusae are usually more or less degenerate and are termed gonophores. Since the gonophore fails to fulfil the purpose for which we believe the Medusa to have been developed we must assume that conditions have so far changed that the same wide scattering of the eggs is not now so necessary as formerly, possibly because the species in question are restricted to particular strips of the shore. It is an interesting fact that those species in which the hydroid persons develop strongly and bud frequently, so as to form a complicated branching system, generally have degenerate Medusae, whilst in those species on the contrary which have free Medusae the hydroid stock buds feebly or not at all and is usually small and poorly developed. *Tubularia larynx* found growing on seaweed is a good example of a form with degenerate Medusae, *Bougainvillia* or *Obelia* of forms with free Medusae.

The Hydromedusae include a large number of families, most of which are represented by small plant-like forms resembling the genera just mentioned, but there are several groups which show marked peculiarities and have been regarded by many zoologists as of co-equal rank with the order although they have doubtless been derived from ordinary Hydromedusae. Of these we may name

(i) the Trachymedusae, (ii) the Narcomedusae, (iii) the Siphonophora and (iv) the Hydrocorallinae. These four groups together with *Hydra* and the Hydromedusae constitute the first primary division of Coelenterata which is termed the Hydrozoa.

In the first group the eggs appear to develop from the planula stage directly into Medusae, missing out the hydroid stage completely, but there is some evidence to show that a more correct interpretation of what happens would be to say that the egg develops into a modified hydroid which is then converted into a Medusa by the appearance of a web connecting the tentacles. The sense organs are specially modified tentacles which are suspended like minute clubs round the edge of the bell. In the Narcomedusae the planula develops into a reduced hydroid which attaches itself to the inner surface of the bell of a Medusa belonging to a different group. Medusoid buds are produced by this person and set free. The sensory organs are short clubs which are freely exposed and the wide baggy stomach occupies the whole under-surface of the umbrella, whereas in the Trachymedusae the sensory clubs are enclosed in pits (Fig. 27, II) and the stomach is small and suspended from the umbrella by a stalk traversed by the radial canals. The name Trachymedusae (Gr. τραχύς, rough) is derived from the circumstance that the umbrella is stiffened by numerous ribs of endoderm cells and the edge has a thick rim of ectoderm. The Siphonophora are stocks consisting both of medusoid and hydroid persons which are not attached to any support but which freely swim or float in the sea. In most Siphonophora some of the medusoid persons known as nectocalyces become locomotor organs and by their rapid pulsations not only drive themselves through the sea, but draw after them the rest of the stock much as an engine draws a train of carriages. Some species, however, like the Portuguese Man-of-war, *Physalia*, have no nectocalyces and float passively about. The popular name of this genus is derived from the shape of the huge air-containing float from which the persons of the colony are suspended. It has been plausibly suggested that the Siphonophora have been derived from planulae which attached themselves to the surface-film of the water instead of to a solid support. The surface-film in consequence of its physical properties acts like an elastic membrane, and in artificial cultures it can often be seen that some planulae of ordinary Hydromedusae do attach themselves to this, and in consequence perish. But if by favourable variations, such as a tendency to cupping of the base and an inclusion of air-bubbles in the cavity, the stock

were enabled to remain suspended, then it would be placed in a very favourable position for getting food, and it has been suggested that the simply floating Siphonophora have thus been evolved from Hydromedusae. If this view be taken, the three chief divisions of Siphonophora represent three successive stages in the adaptation of the group to a pelagic life. Thus the Physaliidae simply float, the Physophoridae float and swim by nectocalyces, whilst the Calycophoridae have lost the float and trust entirely to their powerful nectocalyces.

The Siphonophora are remarkable for the varieties of person which compose their colonies. As varieties of the hydroid person may be named the palpons or tactile persons devoid of a mouth, but showing their equal rank with the nutritive person by the possession of similar tentacles. To the category of medusoid persons belong not only the nectocalyces but the bracts—transparent sheath-like structures sometimes present, which shelter groups of persons. This extreme variety of persons is foreshadowed in the ordinary Hydromedusae. *Hydractinia* for instance, which grows at the mouth of whelk shells inhabited by hermit crabs, has palpons amongst its hydroid persons, but in no case is such extreme diversity attained as among the Siphonophora.

The Hydrocorallinae are really distinguished by the fact that the perisarc which only covers the basal stolons is thick and calcareous. After a while the stolons enclosed in the skeleton die, but fresh stolons are thrown out at higher levels, so the skeleton grows in thickness. The hydroid persons are of two kinds, nutritive persons, gastrozooids, short and with wide mouths, and tactile persons, dactylozooids, which surround each gastrozooid in a circle and which are long and mouthless. Both kinds have short rudimentary tentacles looking like knobs. Most genera produce only gonophores but Millepora give rise to free Medusae devoid of mouth or tentacles in which the genital organs are developed from the manabrum.

Actinozoa.

The Sea-Anemones are representatives of a second division of the Coelenterata, which show a decidedly more complicated structure than the animals just considered. Unfortunately it is very difficult to obtain the ordinary sea-anemones in a sufficiently expanded condition to make out their structure, since when irritated they contract so much as to throw their internal structures into great confusion. Another animal belonging to the same group is the "colonial" species *Alcyonium digitatum*, sometimes called "Dead men's fingers." It

is comparatively easy to paralyse the members of the colony or polyps by adding cocaine, or some similar reagent, to the water in which the colony is living (Fig. 29). If then an expanded polyp be cut off and examined with a lens, we shall be able to make out most of its structure. We notice to begin with that there is a single circle of eight tentacles, each of which has a double row of short branches, so that it looks like a miniature feather; within the circle of tentacles there is, however, no trace of an oral cone; there is instead a flat disc, slightly sunken in the centre, where we find the slit-like mouth. If we look in at the lower cut end of the

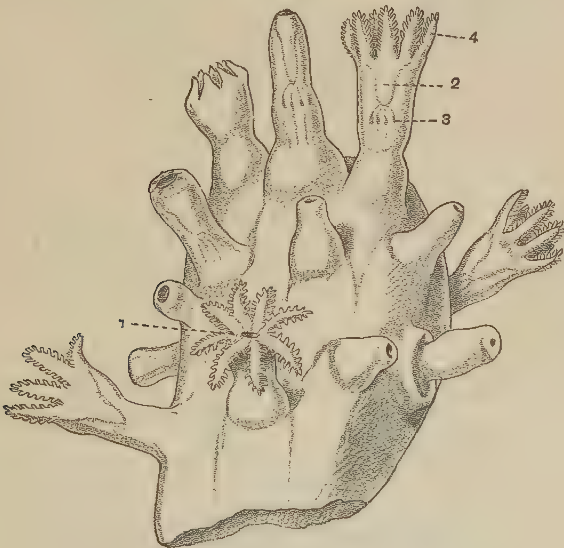
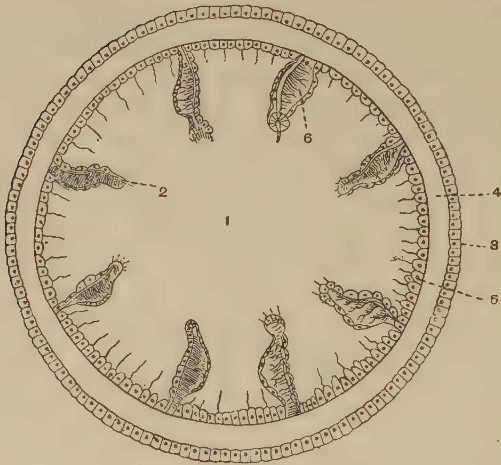


FIG. 29. Part of a colony of *Alcyonium digitatum* × 8, showing thirteen polyps in various stages of retraction and expansion.

1. Mouth.
2. Oesophagus.
3. Mesenteries with reproductive cells.
4. Feathered tentacles.

polyp we shall see that the internal cavity or coelenteron, instead of being a simple cylindrical space like that of *Hydra*, is partially divided into compartments by folds stretching in towards the centre, but not meeting. These folds are called mesenteries, and there are eight of them, corresponding in number (but not in position) with the tentacles (Fig. 30). We shall further see that the mouth does not, as in *Hydra*, open directly into the coelenteron, but leads into a flattened tube which projects into the interior of the body. This tube, the so-called oesophagus or gullet, is really lined by the

Dorsal

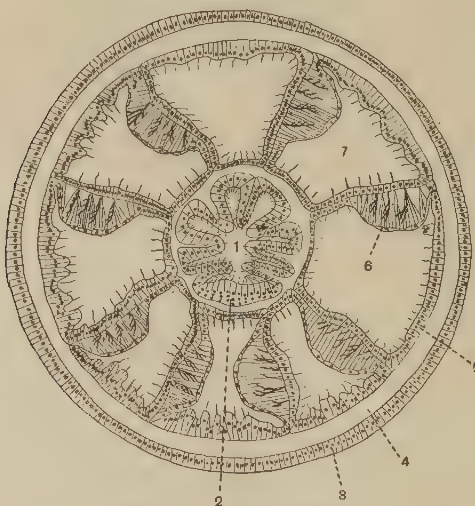


Ventral

Fig. 30. Transverse section through a polyp of *Alcyonium digitatum* below the level of the oesophagus × about 120. From Hickson.

1. Coelenteron. 2. Mesentery with free edge. 3. Ectoderm. 4. Mesogloea or jelly. 5. Endoderm. 6. Muscles in mesentery.

Dorsal



Ventral

Fig. 31. Transverse section through a polyp of *Alcyonium digitatum*, through the region of the oesophagus × about 120. From Hickson.

1. Cavity of oesophagus. 2. Siphonoglyph. 3. Ectoderm. 4. Mesogloea or jelly. 5. Endoderm. 6. Muscles in mesenteries. 7. Intermesenteric cavity.

ectoderm, which is merely tucked in at the mouth. Such a tube is known as a stomodaeum[1]. The mesenteries, although they end freely below, are attached to the sides of the stomodaeum above, so that in this region the coelenteron is divided into a number of compartments, each of which is prolonged into one of the hollow tentacles (Fig. 31).

A microscopic section of such a polyp shows us several other interesting points. We see that we have to deal with the same layers which we met with in *Hydra*, skin (or ectoderm) and coelenteron lining (or endoderm). Between them, however, there is the jelly, which was present as an exceedingly fine membrane in *Hydra*, and which, greatly thickened, formed the substance of the bell of the Medusa. This jelly is fairly thick in the minute sea-anemone we are examining, and here contains cells which have wandered into it from the ectoderm. Some of these cells have the power of secreting thorny rods of lime, termed spicules. These spicules are very abundant where the polyp merges into the general surface of the colony, so that they form a kind of stiff protecting crust round the base of the polyp and over the surface of the colony from which the polyps rise. In the organ-pipe coral, *Tubipora*, the spicules in the lower parts of the polyps are so felted together that they form a set of parallel tubes, suggesting the pipes of an organ; only the upper part of the polyp, where the spicules are not yet closely aggregated, being capable of movement. We have spoken above of the colony as distinct from the polyps, and this use of the word demands some justification. When we were dealing with the Hydromedusae, we used the word colony in the sense of the whole mass of the polyps which cohered together, and which had arisen by the growth of one original polyp. Now in *Alcyonium* and its allies, budding does not take place in quite the simple manner in which it occurs in *Hydra* and its allies. Instead of one polyp growing directly out of another, the coelenteron of the parent sends out a tube lined only by endoderm. This tube grows, pushing the ectoderm before it; but, as between the ectoderm and endoderm there is a thick jelly interposed, the endodermal tube can branch without the ectoderm becoming indented. Where the free ends of these tubes reach the surface, there fresh

[1] "I have proposed to designate this ingrowth...the stomodaeum (στομόδαιον, like πυλόδαιον, the road connected with a gateway) and similarly to call another ingrowth which accompanies the formation of the second orifice (the anus) of the enteron, the proctodaeum (πρωκτός, the anus)." Ray Lankester.

polyps are developed, mesenteries and oesophagus making their appearance. Something like these tubes does, in fact, occur amongst Hydromedusae: a complete colony is found to consist of a number of upright branches ending in polyps but connected at their bases by tubes called stolons which creep along the sea floor: the endodermal tubes of *Alcyonium* may be compared to these stolons, the great difference being that in their case, owing to the thickness of the jelly, the ectoderm is stretched uniformly over a mass of tubes, instead of each tube having its own ectodermal covering as in the Hydromedusae.

Still examining a section of the polyp the next point we notice is the structure of the mesenteries. These end in a free edge below, which is much thickened and folded, and since it stands out in contrast with the rest of the mesentery as if it were an independent structure it has been called a mesenteric filament (Figs. 30 and 32). The cells comprising six of these filaments are very tall and secrete a juice which helps to digest the prey: the remaining two filaments are composed of ciliated cells of moderate height which maintain a constant outward current of water. But there is reason to believe that both kinds of filaments are produced by the downgrowth of strips of ectoderm along the edges of the mesenteries starting from the lower edge of the stomodaeum. The surface of the mesenteries is covered by cells which become very much folded so as to produce a marked projection from the face of the mesentery. The cells of the folded area are all produced into vertical muscle-tails so that together they give rise to one of the powerful longitudinal muscles (Figs. 30 and 31), by which the sudden retraction of the polyp is brought about. The slow expansion is effected by the reaction of the elastic jelly or mesogloea and perhaps also by the pressure exerted on the fluid contained in the body by a layer of circular muscles developed as outgrowths from the endoderm cells of the intermesenteric chambers.

A second difference is found in the position of the eggs and sperm cells. These are developed from the endoderm on the face of the mesenteries, very low down in the base of the polyp and nearer the free edge than the longitudinal muscle. The eggs when ripe are cast out into the coelenteron and pass out by the mouth, though in many species they come in contact with the male cells whilst they are in the coelenteron of the parent.

The gullet has at one side a deep indentation or groove which is lined by powerful cilia (2, Fig. 31). The groove is termed a

siphonoglyph (Gr. σίφων, a tube; γλύφω, to hollow out) and its cilia keep up an inward current of water whilst the rest of the gullet is choked with prey, and so fresh supplies of water charged with oxygen are brought in contact with the lining of the coelenteron and enable it to respire. The two mesenteries with which the lower end is connected are called the directive mesenteries, they are situated opposite to the two ciliated mesenteric filaments. By the cooperation of the latter with the siphonoglyph complete circulation of the water in the coelenteron is maintained. The ectoderm of

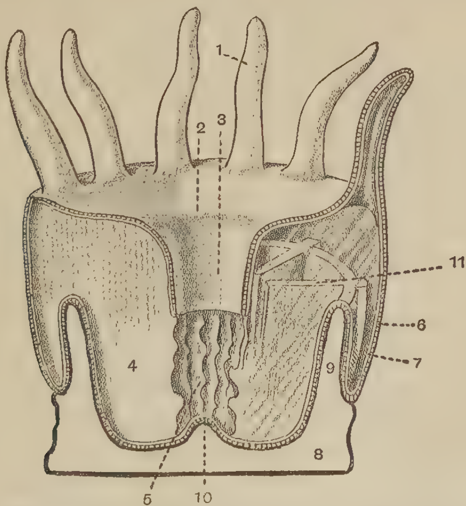


FIG. 32. Semi-diagrammatic view of half a simple Coral, partly after G. C. Bourne. On the right side the tissues are represented as transparent to show the arrangement of the theca and septa; on the left side a mesentery is seen.

1. Tentacle. 2. Mouth. 3. Oesophagus. 4. Mesentery. 5. Mesenteric filaments, free edge of mesentery. 6. Ectoderm. 7. Endoderm. 8. Basal plate. 9. Theca. 10. Columella. 11. Septum.

course gets its oxygen directly from the surrounding water. When the polyp of an *Alcyonium* colony seizes its prey it presses its victim through the stomodaeum into the coelenteron where it is gripped by the inner edges of the eight mesenteries. The stomodaeum and the six glandular mesenterial filaments secrete a juice to be compared to the human saliva which disintegrates the flesh of the victim and causes it to break up into small fragments, these are then swallowed by the endoderm cells covering the mesenteries, especially by those lying immediately behind the filaments.

The ordinary sea-anemones or Zoantharia differ from *Alcyo-*

nium in very many points. The tentacles, hollow as before, are never feather-like but always perfectly simple and round, and there is usually a large number of them arranged in several concentric circles. The mesenteries also are numerous, and extend inwards to different lengths, so that we can distinguish primary mesenteries which join the gullet from secondary ones which do not. Both primary and secondary are usually arranged in pairs, but there is much variety and all that can be universally asserted is that they never exhibit exactly the arrangement shown in Alcyonaria. A very common arrangement is to have six pairs of primary mesenteries and two siphonoglyphs, one at each end. Spicules are never developed and in the ordinary anemones of our coasts there is no skeleton whatever. These commoner forms sometimes, though rarely, bud, but there is another large class of anemones which do form colonies, the buds occasionally arising as in the Hydromedusae from the body of the parent directly but often from the stolons connecting different persons. These colonial anemones form the hard stony masses called coral (Fig. 32). If we look at a piece of coral we can see in it cups with partitions radiating inwards, the whole reminding one of the structure of a sea-anemone: and it was a natural mistake to suppose, as the earlier naturalists did, that the hard skeleton was formed inside the body of the polyps, and that the partitions represented the mesenteries. Of course it is difficult to imagine how the animal could move if it had all that mass of stone inside it. How the corallum or stony skeleton is formed is a matter of dispute. It is certainly situated outside the ectoderm, but whether it is secreted by the ectoderm as a kind of sweat which hardens, or whether the ectoderm cells are calcified and thrown off, or whether the ammonium carbonate, secreted by all animals, precipitates the calcium carbonate of the sea water and so forms the skeleton, is not finally decided. At any rate a calcareous cup is formed in which the polyp sits and the partitions of the cup indent the base of the animal, pushing before them folds of the body wall, which project into the coelenteron between mesenteries, so that the action of the longitudinal muscles is not interfered with.

Coral.

Under the name coral the skeletons of quite a number of different kinds of Coelenterata were included besides Zoantharia.

The so-called millepore corals belong to the first division of the Coelenterata, the Hydrozoa, for Millepora itself gives off quite typical Anthomedusae and the other genera have gonophores.

The so-called organ-pipe coral is, as has been already explained, an Alcyonarian in which the spicules cohere. Various fossil so-called corals, e.g., *Syringopora*, belong to the same category. The red Neapolitan coral of which ornaments are made is also an Alcyonarian, the spicules of which are of a bright pink or red colour and cohere to form a rod in the axis of the colony. In some spots off the coast of Australia the Alcyonaria with coherent spicules are so numerous that they form reefs.

Coral-forming anemones are found all over the world—one genus, *Caryophyllia*, being actually found at low spring tides on the south-west coasts of England: but it is only in the tropics that those species are found which keep on budding and growing with sufficient persistence to build up the great reefs which form the famous coral islands of warmer seas. Of course as soon as the reef is built up to the surface the polyps cease to grow, and then the breakers soon pile up broken off pieces in sufficient quantity to raise the reef above the tide-marks.

Scyphozoa.

A third group of the Coelenterata is constituted by the Scyphozoa (Gr. σκύφος, a saucer). These animals are the larger and better known jelly-fish. They are to some extent intermediate in character between the Hydrozoa and the Actinozoa. Like the latter their genital cells are developed from endoderm, and in the larval condition there are mesenteries, but they do not possess a stomodaeum.

A common British species, *Aurelia aurita*, is in summer often cast by thousands on the southern shores of Great Britain. Viewed from the outside it very much resembles the medusoid persons of the Hydromedusae. Like them it possesses a swimming bell with a circle of tentacles at the margin. There is also a prominent oral cone or manubrium. This however does not bear real tentacles, but the four corners of the rectangular mouth are drawn out into long frilled lips (2, Fig. 33), along the inner sides of which are open grooves leading into the gullet. Perhaps the most marked difference is that the reproductive organs are here, as in the Anemones, swellings of the wall of the stomach: the eggs and spermatozoa are shed into the coelenteron and escape by the mouth. The generative organs have the shape of four semicircular ridges, and along the inner side of each of these there is a row of filaments composed of cells somewhat similar to the cells on the edges of the mesenteries in the anemones (11, Fig. 33). Nothing like these gastral filaments, as they are called, is found in the Hydromedusae. There is,

further, no velum in the Scyphozoa, and there is also no nerve ring. Sense organs however of an exceedingly interesting kind are present.

In *Aurelia*, for instance, there are eight minute tentacles which stick out from the edge of the bell and are covered by special little hoodlike outgrowths of the same (9, Fig. 33). Each of these tentacles contains a hollow outgrowth from the circular canal lined like it by endoderm. The endoderm cells at the tip secrete a mass

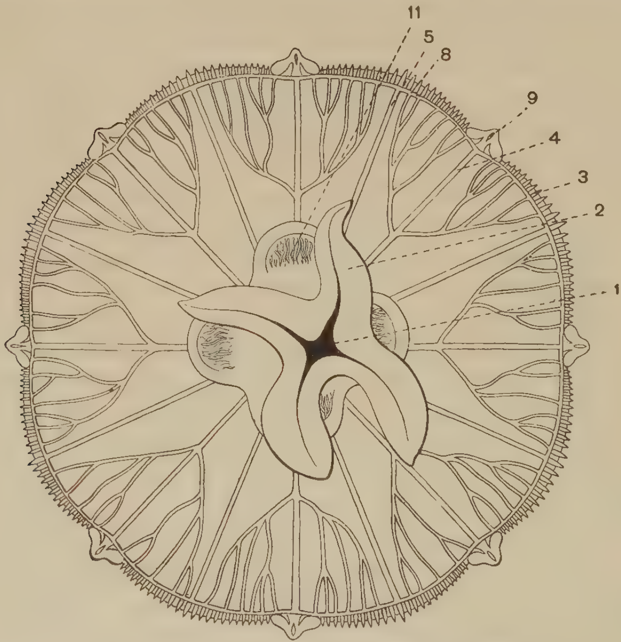


FIG. 33. *Aurelia aurita.* Somewhat reduced.

1. Mouth. 2. Circumoral processes. 3. Tentacles on the edge of the umbrella. 4. One of the branching perradial canals. There are four of these, and four similar interradial canals; the perradial canals correspond to the primary stomach pouches of the Hydra-tuba, the interradial alternate with these. 5. One of the unbranched adradial canals. 8. The circular canal. 9. Marginal lappets hiding tentaculocysts. 11. Gastral filaments, just outside these are the genital ridges.

of calcareous particles: the ectoderm cells at the base of the tentacle have produced nervous fibrillae from their bases and so the tentacle, as it is caused to sway in one direction or another by the weight of its heavy end, affects now some of the nerve fibrillae and now others, and so produces the same effect as the stones in the ear sac of a medusoid, though the construction of the Scyphozoan organ is quite different. In the Trachymedusae and Narcomedusae, how-

ever, as we have already mentioned, sense tentacles similar to those of the Scyphozoa are found. In the Trachymedusae the edges of the hood often join so as to form a sac enclosing the organ, whence the name tentaculocyst (9, Fig. 27, II).

It has been proved experimentally that the ordinary stimuli which cause the rhythmical pulses of the bell proceed from these tentaculocysts, so that they act like minute brains. The co-ordination of the stimuli proceeding from the eight centres is effected by a very thin diffuse sheet of nerve fibrillae on the under surface of the bell. These nerve fibrillae are outgrowths of star shaped cells very like the nerve-cells of *Hydra*.

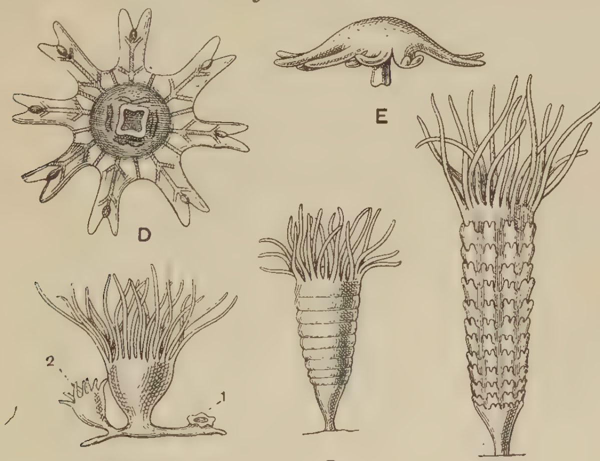


Fig. 34. Strobilisation of *Aurelia aurita*. From Sars.

A. Hydra-tuba on stolon which is creeping on a Laminaria. The stolon is forming new buds at 1 and 2. B. Later stage or Scyphistoma × 4. The strobilisation has begun. C. Strobilisation further advanced × 6. D. Free swimming Ephyra stage × 7·5, seen from below. E. The same seen in profile × 7·5.

It has been mentioned above that the reproductive organs are swellings of the endoderm. The central space or "stomach" is a wide sac occupying the centre part of the bell and not, as in the Hydromedusae, confined to a large extent to the oral cone. In *Aurelia* this space is produced into four lobes, and in the floor of each lobe is one of the reproductive organs. From the edges of the stomach a number of branching canals lead out into the circular canal (4, Fig. 33), all these tubes being, as it were, burrows in a continuous sheet of endoderm cells, which is formed in the same way as the endodermal lamella of the Hydromedusae by the development

of lateral fringes on the walls of radial pouches and the union of these fringes with one another.

When the eggs fall out of the mouth they are caught in little pockets and there develop into little planulae. These, as usual, become free and swim about, and finally each fixes itself and develops into a little polyp, called a Hydra-tuba, not unlike a *Hydra* in appearance (A, Fig. 34), but there are nevertheless important points of difference. Thus there is no oral cone but a flat oral disc, in the centre of which the mouth opens into the coelenteron. The latter has four ridges projecting into it, the lower edges of which are free while the upper ones are joined to the oral disc. These ridges being produced by the folding of the endoderm layer they are double and contain between their two limbs a space filled with jelly. Into this space a prolongation of the ectoderm of the mouth disc grows down so as to form a "septal funnel." The cells composing the septal funnel secrete longitudinal muscular fibrils, and thus four powerful septal muscles are formed which serve to shorten the Hydra-tuba. The hydroid persons of the Hydromedusae have also longitudinal muscles but these are disposed in a uniform sheet round the polyps in question and belong to the ectoderm cells forming the sides. During a large part of the year the Hydra-tuba multiplies by budding, just as a *Hydra* does, but at certain seasons it undergoes a very remarkable change (B and C, Fig. 34). The oral disc flattens out very much and its edges become drawn out into lobes, the tentacles at the same time dropping off. A short oral cone is developed from the centre of the disc, the mesenteries become perforated and finally the whole flattened-out top of the Hydra-tuba breaks off and swims away. This is known as an Ephyra larva (D and E, Fig. 34). It leads a free life and gradually develops into a large jelly-fish. But long before the primary oral disc has become free, the part of the Hydra-tuba next below has been growing out so as to produce a similar disc. This process, called Strobilisation (Gr. *στρόβιλος*, a whorl), is repeated until the Hydra-tuba resembles a pile of saucers, in which state it is called a Scyphistoma (Gr. *σκύφος*, a saucer).

We can get some idea as to how this extraordinary development may have arisen on the following hypothesis:—The original Scyphozoan was probably an organism like a hydroid of the Hydrozoan genus *Tubularia* with a wide head and narrow base. In this top the generative organs were developed, and when the eggs became ripe it broke off and wandered away in order to disperse the species.

The lower part of the hydroid regenerated the head, exactly as a *Hydra* can do if the head with its ring of tentacles be cut off. Later this process of renewal became hurried on until it commenced before the separation of the head was complete and thus we have the Scyphistoma stage. It is a strong support of this

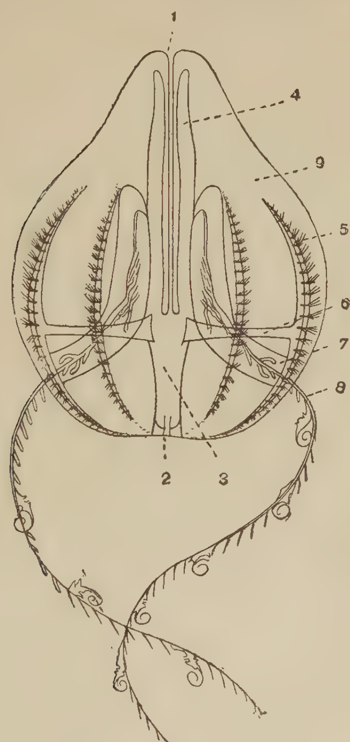


FIG. 35. *Hormiphora plumosa*. After Chun. Side view.

1. Mouth leading into stomach. 2. Aboral pole with sense organ. 3. Funnel. 4. Paragastric canal running back towards oral pole. 5. One of the eight bands of fused cilia. 6. One of the eight canals running towards 5. 7. A tentacular pouch. 8. A tentacle. 9. Gelatinous tissue.

theory that the polyps of the genus *Tubularia* are often cast off in the winter-time and are regenerated from their basal stumps in the spring.

Ctenophora. A fourth great division of the Coelenterata is constituted by the animals called Ctenophora (Gr. κτείς, κτενός, a comb). These are widely different from Hydromedusae, Actinozoa, and Scyphozoa. They never bud and they have no thread

cells. In place of these there are gripping or adhesive cells covered with a secretion by which they adhere to the prey. They are often ripped off in the struggles of the prey. They are each provided with an elastic tail embedded in the jelly which pulls in the object to which they have adhered. The Ctenophora are free swimming but their locomotion is performed not by the agency of muscular bands but by eight bands of cilia which run like meridians of longitude over the generally oval body from the mouth to the opposite pole (5, Fig. 35). The cilia in each band are arranged in short transverse rows, and the cilia in each row are joined at the base and free at the tip. So each row has the form of a comb, and thus the name Ctenophora, comb-bearers, is seen to be appropriate. Further the principal sense organ is situated in the centre of the end of the animal opposite to the mouth at the spot where the bands of thickened ectoderm which carry the combs converge. These thickened ridges of cells are often termed "ribs." If we compare the animal to a globe, the end at which the mouth is may be called the oral pole, the opposite end the aboral pole (2, Fig. 35). The sense organ at the aboral pole is a plate of thickened ectoderm, the cells of which have developed nerve tails. Similar nerve tails are developed by the bands of ectoderm which carry the combs. Underneath the ectoderm in the spaces between the ribs there is a network of fine nerve fibres derived from scattered nerve cells like those of *Hydra* or *Aurelia*. The cells at the edge of the plate carry cilia fused with one another which arch over the plate and cover it like a tent. Inside is a calcareous ball supported on four curved bars, each made of conjoined cilia, borne by some of the inner cells. This ball acts as a balancing sense organ. If the animal inclines to one side the ball will bear heavily on the support on that side, and stimulate thus the corresponding ribs, which will thus act more vigorously than the rest and tend to restore the vertical position.

Like Actinozoa, Ctenophora have a well-marked stomodaeum, and the true coelenteron is represented by a series of branching canals, the central one being termed the funnel (3, Fig. 35). The funnel and stomodaeum are both flattened but in planes at right angles to one another. The funnel gives off (1) two canals, the so-called excretory canals, which open at the sides of the sense organ; (2) two canals, paragastric, running back towards the mouth parallel with the stomodaeum (4, Fig. 35); (3) two canals running each to the base of a branched tentacle, which can be retracted

within a pouch (7, Fig. 35). This branched tentacle is covered with adhesive cells, there is one on each side of the animal. These last mentioned canals are termed perradial. Each perradial canal gives off two lateral branches termed interradial canals and each interradial canal finally gives off two so-called adradial canals (6, Fig. 35) which lead into the meridional canals running under the ribs, from the cells lining which both ova and spermatozoa are produced, Ctenophora being hermaphrodite. Between ectoderm and gutwall is a gelatinous substance which differs from the jelly of other Coelenterata in having numerous cells with long processes embedded in it. These processes connect the cells with one another and with the ectodermal and endodermal cells. Many of them are contractile—i.e. have become muscular—and thus the jelly of the Ctenophore is traversed by a network of thread-like muscles. The commonest British form is *Hormiphora plumosa*, which sometimes appears in shoals in the seas washing the Atlantic coast of Britain on the one hand and America on the other. The Ctenophora are good examples of what are called pelagic organisms, that is to say, organisms which pass their whole life from the egg to the adult condition floating at or near the surface of the sea. Such organisms are the only ones which are found in mid-ocean. Nearer the shore the waters are filled by a profusion of other animals, but these turn out on examination to be largely composed of forms which in some period of their existence are adherent to or creeping on the bottom. Other purely pelagic groups are the Siphonophora, the Trachymedusae and the Narcomedusae.

The Ctenophora contain many forms which differ widely in appearance from *Hormiphora*—for instance the *Cestum veneris*, or Venus's girdle, a beautiful transparent ribbon-like creature, a foot or so in length and two or three inches wide. On close examination the reason of this diversity of shape is found to be that the Ctenophora are not really radially symmetrical, but doubly bilaterally symmetrical. That is to say, not only right and left sides are like one another but also the back and belly are alike, but at the same time different from the sides. The difference between back and belly on the one hand and the two sides on the other is slight in *Hormiphora* but very strongly marked in *Cestum veneris*.

Phylum COELENTERATA.

The classification of the Coelenterata is as follows:

Class I. Hydrozoa.

Coelenterata without mesenteries or gullet lined by ectoderm: genital cells derived from ectoderm.

Order 1. **Hydrida.**

Only hydroid persons present, not permanently attached but capable of locomotion: the buds become free.

Order 2. **Hydromedusae.**

Composite fixed colonies of hydroid persons from which medusoid persons are budded off.

Sub-order (1). **Gymnoblastea** (Anthomedusae). Perisarc confined to the base of the hydroids: medusoids have eyes and bear gonads on the manubrium. Ex. *Bougainvillea, Tubularia.*

Sub-order (2). **Calyptoblastea** (Leptomedusae). Perisarc expanded to form cups called hydrothecae, into which the heads of hydroid persons can be retracted: medusoids have ears and bear gonads on the under side of umbrella. Ex. *Obelia.*

Sub-order (3). **Hydrocorallinae.** Perisarc thick and calcareous, surrounding chiefly the stolons which are given off at various levels and form a thick mass. Hydroid persons of two kinds nutritive and tactile. These are closely allied to the Gymnoblastea of which they ought to form a sub-division. Ex. *Millipora.*

Sub-order (4). **Narcomedusae.** The hydroid is fixed to the inside of the bell of another Medusa. The manubrium of the Medusa is poorly developed, and the wide stomach occupies the under side of the bell. The sense-organs are reduced tentacles projecting at the edge of the bell.

Sub-order (5). **Trachymedusae.** Forms in which the hydroid does not bud but develops directly into a Medusa in which there is a long manubrium traversed by the radial canals, the lower portion of which contains the stomach. The sense-organs are reduced sense-tentacles enclosed in sacs of ectoderm.

Sub-order (6). **Siphonophora.** Free-swimming colonies consisting of hydroid and medusoid persons in which the base is modified into a float or some of the medusoids are transformed into swimming organs, or both arrangements are combined.

Class II. Actinozoa.

Solitary or colonial Coelenterata with gullet lined by ectoderm: coelenteron provided with radiating mesenteries: genital cells derived from endoderm.

Order 1. **Alcyonaria.**

Eight mesenteries and eight fringed tentacles: spicules in the jelly. Ex. *Alcyonium*, *Tubipora*, *Corallium*.

Order 2. **Zoantharia.**

Mesenteries usually in pairs, either six pairs or some multiple of six: tentacles conical: no spicules but often an external calcareous skeleton formed by the ectoderm.

Class III. Scyphozoa.

Coelenterata with alternation of generations: mesenteries present in young, but later becoming absorbed: oral part breaks loose and becomes developed into a free-swimming organism externally resembling a medusoid: the stalk of the original polyp reproduces the lost parts. Ex. *Aurelia*.

Class IV. Ctenophora.

Very widely different from the two preceding divisions: free-swimming animals with a sense organ and nervous disc of skin at the pole opposite the mouth: swim not by muscular contractions but by vibrations of eight longitudinal bands of cilia radiating from nervous disc, which bands consist of successive transverse rows of cilia, the cilia of each row fused at base so as to form a comb-like structure: only two tentacles, a gullet lined by ectoderm: stomach represented by a system of branching tubes. Ex. *Hormiphora*, *Cestum*.

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CHAPTER IV

PHYLUM PORIFERA

General description.

The group of the sponges or Porifera occupies an almost isolated position in the animal kingdom. Sponges agree, it is true, with Coelenterata in exhibiting cellular structure and having their protoplasm arranged in tissues; and further in the fact that all the internal cavities of the body are in communication with one another, so that both Coelenterata and Porifera might be described as systems of branched tubes. A closer inspection however reveals the fact that the tissues of the Porifera are very different from those of Coelenterata and originate in a different way from the larva, so that the opinion is gaining ground that whereas most, if not all, of the higher groups of animals have descended from ancestors which had we seen them we should have classed as Coelenterata, Porifera on the other hand have been independently derived from Protozoa.

In Coelenterata the colonies can be analysed into persons (medusoids or hydroids) and stolons, and many of the Porifera show a like aggregation of persons. But in many forms it is impossible to suggest how many individuals are contained in the branch system of a single aggregate since all distinctness of individuals is lost. Further analysis shows that the apparent persons or units, even when most clearly demarcated, are of very varying morphological value.

Leucosolenia.

The salient peculiarities of sponges will be best appreciated by a short description of one of the simplest types known, a sponge called *Leucosolenia*, which is common on most clean rocky shores.

In this animal we can recognise a foundation consisting of a network of horizontal stolons, adherent to some foreign object, from which a number of upright tubes spring. Each upright tube ends in a large opening, termed the osculum (1, Fig. 36), which can be closed if the animal be irritated and which in *Leucosolenia* is

partly closed by a perforated membrane. This opening, which at first sight recalls the mouth of *Hydra*, is really used for a quite different purpose. It is an efferent opening (Lat. *effero*, I carry out) and from it the water which has passed through the animal is expelled. Water enters the internal cavity through a multitude of very fine pores in the walls of the tube (Fig. 37, and 1, Fig. 39): it is the universal presence of these pores which gives the name Porifera to the group.

The wall of the tube is made up of two layers, but we must guard ourselves against rashly comparing these with the layers of the body wall of *Hydra*, and hence it is better to avoid the names ectoderm and endoderm and adopt the terms dermal and gastral layers.

FIG. 36. View of a branch of *Leucosolenia* sp., showing the sieve-like membrane which stretches across the osculum. The lower part of the sponge shows spicules only × 10. From Minchin.

1. Osculum with sieve-like membrane stretched across it.

The dermal layer consists of flat cells which cover the external surface and extend for a short distance inside the osculum, and of cells termed amoebocytes from the resemblance of their movements to those of an *Amoeba*: the whole of the rest of the tube and the stolons are lined by a tissue consisting of peculiar cells called choanocytes (Gr. χόανος, a funnel; κύτος, a hollow vessel), or collar cells, which alone constitute the gastral layer (3, Fig. 37 and Fig. 38). Each of these is cylindrical and provided with a funnel-shaped transparent rim called the collar, turned towards the cavity of the tube. The collars of adjacent cells are not

normally in contact, and the outer part of the cell bodies are widely separate, so that here the distinctness of the elements of a cellular tissue is carried to an extreme. From the centre of each collar a long flagellum arises, and it is by the action of these flagella

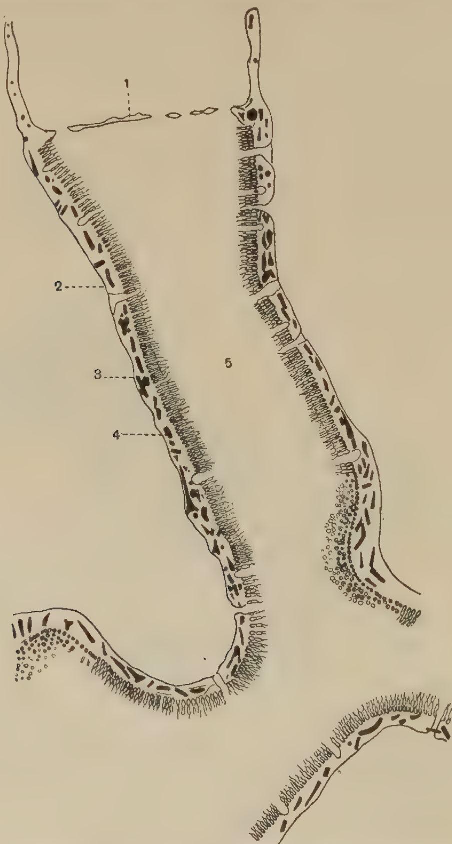

Fig. 37. Vertical section through an osculum with sieve-like membrane, and a tube of *Leucosolenia* sp. Highly magnified. From Minchin.

1. Sieve-like membrane. 2. Outer layer. 3. Flagellated or collar cells (choanocytes). The pointer should have been continued to indicate the cells lining 5. 4. Spicules. 5. Internal cavity.

that water is drawn in through the pores. The sponge lives on the organisms carried in by the current; these appear to be carried within the collars by the minute whirlpools produced by the individual flagella: they adhere to the collars and are swallowed by them and digested by the cells. It will be seen that the collar is

a real living structure, not a cuticular tube, such as the hydrotheca of a calyptoblastic hydroid, and this is further illustrated by the fact that it is withdrawn by the collar-cell under certain conditions.

The water after being exhausted of its food is expelled through the osculum, carrying with it all excreta.

The outer layer of the body-wall consists, in the ordinary condition of the sponge, of flattened cells. These however, especially in the region of the osculum, have the power of changing their shape so as to become shorter and thicker; in a word they can contract, although they show no trace of the fibrillae found in all muscle and in the muscle tails of the contractile cells of Coelenterata. The contraction is slow, not quick, as in true muscle.

FIG. 38. Section of flagellated chamber of *Spongilla lacustris*, showing the flagella and collar cells × 1500. From Vosmaer.

1. Nucleus. 2. Vacuole. 3. Opening into the inner space of the sponge.

It has been proved that the pores are formed by large dermal cells, the porocytes, which extend in from the outer layer and push aside the choanocytes, and then become hollowed out.

Between the two layers is found a certain amount of secretion which may be termed jelly, in which in many sponges a large number of cells is found. These form a portion of the dermal layer, and are, for the most part, amoeboid. Some of these probably act as carriers of food and possibly of excreta from one layer to the other. Others at first very similar give rise to ova and spermatozoa. A third class called scleroblasts—derived in *Leucosolenia* from the flat cells which cover the surface, but not so derived in all sponges—secrete the rods which form the skeleton and which are

termed spicules (Fig. 36, and 6, Fig. 39). In *Leucosolenia* these are calcareous and have three rays, more or less in one plane—a shape technically named triradiate. One limb is usually directed parallel with the long axis of the tube, and often bears a fourth ray or spine in which case the spicule is quadriradiate. The spicules although remaining unconnected are numerous enough to form a loose meshwork.

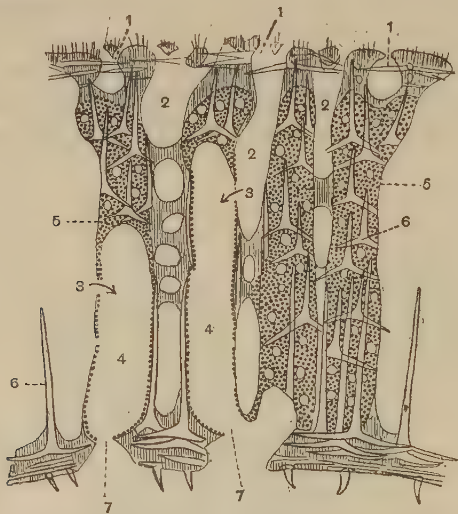

Fig. 39. Section of a portion of *Grantia extusarticulata*. Highly magnified. From Dendy.

1. Openings of the inhalant canals. 2. Inhalant canal. 3. Openings of inhalant canals into flagellated chamber (prosopyle). 4. Flagellated chamber. 5. Flagellated or collar cells (choanocytes). 6. Spicules. 7. Exhalant opening of flagellated chamber.

Complex Sponges.

The most important points in which the higher sponges differ from *Leucosolenia* are the folding of the outer and inner layer, the restriction of the choanocytes to small portions of the latter, and the differentiation of the body into distinct regions.

A common sponge on the British coast, *Sycon* (*Grantia*) *compressum*, will illustrate the first step in this complication. This animal has the form of a series of flattened thick-walled upright tubes. The layer lining the central cavity consists of flattened cells, but from this cavity pouches lined by choanocytes extend out into the substance of the wall. These flagellated chambers, as they are often called, communicate with the exterior by a series of

inhalant or afferent (Lat. *ad*, to; *fero*, I carry) canals which intervene between them and into which the pores open (Fig. 39).

When a sponge becomes still more complicated the central cavity becomes broken up into a series of branching canals, which are termed exhalant or efferent, and the flagellated chambers become small and rounded (Fig. 38), each often connected only by a single opening or prosopyle (Gr. πρόσω, forwards; πύλη, a gate) with the afferent system of canals. Numerous oscula are found in one sponge mass, so that no pretence of discriminating the individual can be made.

A still further complication arises from the presence of subdermal spaces. These are wide cavities immediately beneath the surface of the sponge into which the pores open and from which the afferent canals take their origin. In this way a rind or crust of the sponge can be separated from a deeper part containing the flagellated chambers.

Larva. The larvae of sponges are best understood by a short description of the simplest form, viz. the larva of *Oscarella*. This has the form of a simple hollow sphere of ciliated cells like the planula of Coelenterata in its first stage. The cells at one pole lose their cilia, become pigmented and granular and then the larva fixes itself by the ciliated pole. The whole animal flattens and the granular cells extend over the ciliated cells, which become tucked into the interior and there arranged as an inner lining to a cavity. The flagellated chambers of the adult arise as small pocket-shaped outgrowths from this cavity and the osculum is a later perforation. The ciliated cells are eventually restricted to these chambers, where they form the choanocytes and all the rest of the sponge is formed from the granular cells.

Other larvae differ from that of *Oscarella* in the early multiplication of granular cells which form a solid mass at one end of the larva, and often, indeed generally, this mass is of such extent as to project into the interior. To compensate for greater dead-weight, so to speak, the ciliated layer—the locomotor organ of the larva—becomes extended so as to surround the granular material, so that we are presented with the remarkable phenomenon of the internal layer of the larva bursting forth and becoming the outer layer of the adult. This is the case in the larva of *Leucosolenia*. In the larvae of other calcareous sponges, the ciliated cells at first surround the granular cells, but the latter are afterwards exposed and the larva in this form has been called an amphiblastula.

In the case of most of the Demospongiae the ciliated cells nearly, but not quite, surround the granular cells, and these last often contain a number of spicules ready formed in a central bundle which are scattered in all directions when the sponge flattens on fixation. Comparing the development of a sponge with that of the planula of a Coelenterate we see that in the first the ciliated cells form the internal layer, in the second the external layer of the adult; in the first the animal fixes itself by the pole at which the invagination or intucking of the cells destined to form the inner layer takes place, in the Coelenterate at the opposite pole; so that if Coelenterata and Porifera had an ancestor in common it could only have been an animal like the organism *Volvox*, consisting of a single sphere of cells—in a word were it living now it would have been classed as a Protozöon.

The study of the development of sponges like *Sycon* shows that at first, after the metamorphosis, the sponge has the form of *Leucosolenia*, i.e. a simple cylinder lined by choanocytes. The flagellated chambers arise as horizontal cylindrical branches on the primitive chamber and soon become so numerous that their walls come into contact and the afferent or inhalant canals are simply the crevices left between these chambers. As the chambers develop, flattened cells come inwards from the pores and displace the choanocytes from the walls of the central chamber into the flagellated chambers.

Porifera then may be defined as animals consisting of branch-systems of tubes, the principal openings of which are exhalant, whereas the inhalant openings are minute perforations of the walls. The wall consists of two layers; some cells of the inner layer have the form of choanocytes, whilst the skeleton consists of siliceous or calcareous needles formed by cells of the outer layer which wander in, or of spongin. There are never any thread-cells or differentiated muscle or well-marked nerve-cells, nor any such organs as tentacles.

Sponges are by some of the best authorities divided into three main classes, viz.:

Class I. Calcarea.

This group includes all those sponges with calcareous spicules and comparatively large flagellated chambers.

It is divided into two main orders:

Order 1. **Homocoela.**

Sponges consisting of tubes lined throughout with choanocytes.

Order 2. **Heterocoela.**

Sponges in which the choanocytes are restricted to special chambers—which may be cylindrical as in *Grantia* or spherical as in *Leucandra*.

Class II. Hexactinellidae.

Sponges in which the skeleton consists of a coherent network of siliceous spicules each consisting of three axes placed at right angles to one another. The flagellated chambers are large and cylindrical but are separated from the central space by a system of canals. The central space may be deep and narrow and covered with a plate pierced by numerous oscula, or short, open and shallow.

These sponges inhabit as a rule very deep water and most species are provided with a tuft of long needle-like spicules which root them in the soft mud which forms the bottom of the sea at these depths. It is a most interesting fact that the flints which form regular rows in our English chalk have been proved in many cases to contain the remains of Hexactinellid sponges. As the chalk is a deposit on the sea-bottom similar to the globigerina ooze on the floor of the Atlantic one would expect it to have been richly sown with these sponges.

Class III. Demospongiae.

These sponges derive their name from the fact that their spicules, which are always siliceous, are arranged in cords so as to form a network traversing the substance of the sponge. The spicules composing these cords are nearly always cemented together by a horny elastic material called spongin. The flagellated chambers are always extremely small and there is never a central chamber. Besides the skeletal spicules, as those composing the cords are called, smaller ones called flesh spicules are scattered singly in the intervals of the network.

There are several exceptional genera in which interesting modifications occur.

Oscarella is totally devoid of any skeleton and has the appearance of a whitish yellow scum on the rocks to which it adheres. *Euspongia* possess spongin cords but these cords have no spicules in them, and for this reason it can be employed for domestic purposes.

Two fresh-water species, namely, *Spongilla lacustris* with a bush like appearance and *Ephydatia fluviatilis* with an encrusting form, are often found growing on the side of canals and on the timbers of river-locks or weirs in Great Britain. The two species are bright green when they grow in the light, but they are pale flesh-colour when they grow in the shade. In Canada similar species adhere to stones in the river St Lawrence.

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CHAPTER V

PHYLUM PLATYHELMINTHES

THE name Platyhelminthes (Gr. πλατύς, flat; ἕλμινς, ἕλμινθος, a worm) means simply "flat worms." The word worm is a popular expression not capable of any very exact definition. It connotes in the popular mind a low wriggling animal without conspicuous appendages. The animals belonging to the phylum of Platyhelminthes are almost always of a flattened shape. They agree with the Coelenterata in possessing only one opening to the alimentary canal—and this, as in Coelenterata, functions as a mouth through which nourishment is taken in. Between ectoderm and endoderm there intervenes a mass of tissue which strongly recalls the tissue making up the body of a Ctenophore. This tissue is called parenchyma and its basis is a mass of stellate cells embedded in a ground substance. The processes of many of these cells are metamorphosed into muscle fibres, and these muscle fibres are arranged in longitudinal, circular and vertical layers. The Platyhelminthes are distinguished from Ctenophora by three main features. (1) They have a definite nervous system separated from the ectoderm, which consists of two large closely connected masses in the anterior part of the body called the brain, from which two bands of nerve fibres run backwards along the two sides of the body which are termed lateral nerve cords. The swellings termed ganglia (Gr. γάγγλιον, a knot) are produced by an accumulation of the bodies of nerve cells. The cords consist mainly of their outgrowths which constitute nerve fibres, although cell bodies are not entirely restricted to the ganglia but are also scattered along the course of the cords in lesser numbers. (2) They possess reproductive organs which do not discharge directly either to the exterior or into the alimentary canal, but which are connected with the exterior by long complicated tubes termed genital ducts. (3) They possess a definite excretory system. With regard to the last-named point it is to be noted that

in all the animals which we have so far studied excretion seems to be performed by each cell for itself. In a sense this is true of all animals—all protoplasm must be continually producing excreta so long as it is living and these excreta must somehow be got rid of. So long as protoplasm is arranged (as in most Coelenterata) in the form of thin layers of cells lining tubes, excreta are easily voided into the cavities of the tubes, or in the case of ectodermal cells directly to the exterior.

When however we have thicker masses of cells such as are met with in the parenchyma of Platyhelminthes, then their excreta must pass into the fluid in which they are bathed, i.e. the fluid that fills the space between ectoderm and endoderm, into which the cells forming the parenchyma pass. As the percentage of excreta in this fluid rises it tends to become poisonous to the cells—unless the excreta are in some way crystallised out from it. This then is the function of an excretory organ—it precipitates the excreta in the body-fluids in its cytoplasm. The precipitated excreta may be retained in the excretory cell as insoluble granules till it dies and drops off, or they may be redissolved and cast forth as an external secretion by that cell. The ectoderm seems to have been the original excretory organ, and the first distinct excretory organs which we encounter in Platyhelminthes for the first time appear to arise as tubular ingrowths of ectoderm into the parenchyma. These ingrowths branch repeatedly and each branch terminates in a peculiar cell known as a flame-cell or solenocyte. Such a cell is hollowed out by an extension of the excretory tube which ends blindly within it and is lined by a cuticular substance. From the blind end there grow out one or more flagella which project into the tube and by their vibration suggest the flickering of a flame. Water passes through

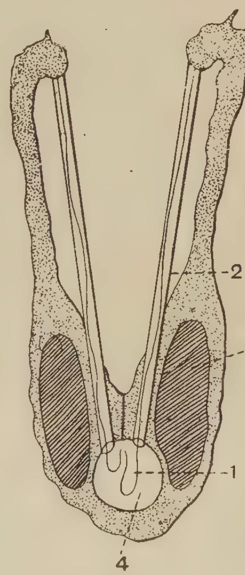


FIG. 40. Two flame-cells or solenocytes from the nephridium of an Annelid worm. (After Goodrich.)

1. Flagellum of the flame-cell. 2. Branch of the nephridial tube leading into the flame-cell. 3. Nucleus of flame-cell. 4. Main tube of the nephridium.

the thin wall of the tube by osmosis and dissolves the excreta which the cells forming the wall of the tube cast out into it. Such a branched tube ending in flame-cells is known as a nephridium (Gr. νεφρίδιον, little kidney).

Class I. Turbellaria.

The Turbellaria are free-living animals, and as a rule swim about in the sea or in fresh-water ponds or streams. A few, however, have taken to living amongst moist earth, and some species, e.g., *Bipalium kewense*, are occasionally met with in hot-houses all over the world, being probably imported with the roots of some tropical orchid or fern. Other species of land Turbellaria are common in the Tropics.

Turbellaria are all very soft animals and capable of considerable change of outline. In their native habitat they are not easy to see, many of them having colours which imitate the sea-weeds, etc., amongst which they live, and many appear only at night from their hiding-places. If, however, a bunch of red sea-weed be shaken out in some clean sea-water in a white china dish, as a rule many of these animals can be seen swimming with an undulating motion like a Sole or clinging to the sides of the dish.

One of the commonest species in the fresh-water ponds of Great Britain is *Mesostoma ehrenbergii*, a flat leaf-like organism, perhaps half an inch long, the transparency of whose tissues permits at times the examination of some of the internal organs. The whole of the outer layer of cells—the ectoderm—bears innumerable cilia, by the action of which the animal glides slowly along when it does not swim by the undulations of its whole body. Within this ectoderm are certain circular and longitudinal muscle-fibres, and these surround a mass of cells called the parenchyma. As just explained the muscular fibres are only specialised outgrowths of certain of the parenchyma cells.

The ectoderm cells secrete a great deal of mucus, mingled with which are a number of little rod-like bodies called rhabdites. The exact use of these is not clearly known; in their formation they recall the nematocysts of the Coelenterata. Like the nematocysts they are extruded on irritation. The mucus forms a bed over which the animal moves and in which the cilia work, so as to propel the animal.

The mouth of the *Mesostoma* is, as its name indicates, near the centre of the body, on the ventral surface. It leads at once into a pharynx with very muscular walls which can act like a sucker.

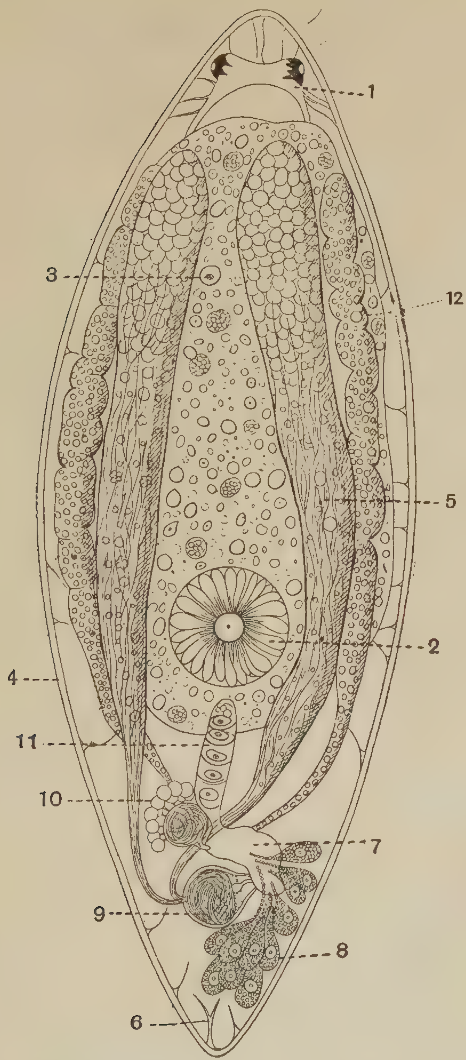


FIG. 41. *Mesostoma splendidum*, drawn from a compressed individual; the cilia and rhabdites are omitted. Magnified. From von Graff.

1. Brain, showing two eyes. 2. Pharynx surrounding the mouth. 3. Food vacuole in an endoderm cell. 4. Ectoderm. 5. Testis lying above alimentary canal, showing developing spermatozoa. 6. Muscle fibres. 7. Genital atrium. 8. Glands of the genital atrium. 9. Penis. 10. Shell-glands surrounding the spermatheca. 11. Germarium. 12. Vitellarium.

This pharynx can be withdrawn into the body or pushed a little way out of the mouth. The chamber in which it lies, and which gives it room to play in and out, is an ectodermal pouch called the pharynx-sheath. This is small in *Mesostoma*, but in other Turbellarians it may be much larger, and the pharynx is consequently capable of stretching out a long distance. This is the case, for instance, with the fresh-water genus *Planaria* (Fig. 42).

Certain glands, called salivary glands, open into the cavity of the alimentary canal at the inner end of the pharynx, and then the cavity opens into the stomach, which is a sac-like structure with no other opening than the mouth lying in the centre of the body. The cells lining this cavity are, like the endoderm cells of *Hydra*, amoeboid, and they take up particles of food into themselves in the same way that an *Amoeba* does. This primitive form of digestion has been lost in most of the higher animals, where the digestive cells pour out solvent fluids into the cavity of the alimentary canal, and the food is rendered soluble in this cavity before being absorbed. In the Turbellaria, as in the Coelenterata, this secondary method of digestion coexists with the amoeboid method.

Mesostoma is carnivorous and eats small worms, minute crustacea and insect larvae. It uses its mucus to ensnare and entangle its prey. Its method of devouring them resembles the habits of the Starfish. It holds them fast by means of the pharynx, using this as a sucker. The so-called salivary glands secrete a strong digestive ferment which rapidly dissolves the flesh of the victim, reducing it partly to a fluid condition and partly to a disintegrated mass of particles. There is no vascular system to distribute the digested food to the different parts of the body, so that these products must be passed from cell to cell through the solid body until they arrive where they are needed. The undigested parts are passed out through the mouth.

The two main ducts of the excretory or "water-vascular" system open near the sides of the mouth, each then passes upwards towards the dorsal surface and divides into two longitudinal vessels, one running towards the head, the other towards the tail. These four longitudinal branches give off innumerable finer ones, which subdivide until each branchlet ends in a flame-cell. These latter are very minute and require a high power of the microscope and very careful focusing to see. We may thus say that the excretory system consists of a pair of very greatly branched nephridia.

The nervous system consists of a large ganglion called the brain,

divided by a shallow depression into two lobes. It is situated in front of the mouth near the anterior end of the animal, embedded in the parenchyma. It gives off a pair of nerves which run forward to the tip of the body, and another pair of rather stout nerves which run back, one on each side of the pharynx, to the tail. The nerves give off fine branches which are distributed all over the body. A pair of eyes of a simple structure lie on the upper surface of the brain.

Mesostoma like *Hydra* is hermaphrodite. Both eggs and spermatozoa are expelled from a single genital pore situated behind the mouth. This pore leads into an ectodermic sac called the genital atrium.

The male organs consist of two long sac-like testes which lie above the alimentary canal and are directly continuous with short ducts which connect them with the genital atrium and are termed the vasa deferentia (Lat. *vas*, vessel; *dēferens*, carrying down). These ducts unite to form the muscular tube called the penis, which communicates with the genital atrium through which it can be protruded. It is inserted into the genital atrium of another individual and in this way the spermatozoa are transferred from one individual to another. This forcible transference of spermatozoa from the male to the female is termed copulation. The proximal portion of the penis is swollen up to form a bulb called the vesicula seminalis, in which the spermatozoa are stored up before being transferred to another individual.

The female organs consist of a large ovary on each side, divided by constrictions into numerous lobes; these are not well marked in the species represented in Fig. 41. The whole of one ovary and the greater part of the other produce only small round eggs incapable of development termed yolk-cells, these portions of the ovaries being called yolk-glands or vitellaria. The yolk-cells serve as food for the developing eggs. The basal lobe however of one of the ovaries (11, Fig. 41) produces ova capable of development; this is the ovary (*sensu stricto*) or germarium. The two oviducts, or, as they are generally styled, the vitellarian ducts, are directly continuous with the yolk-glands and lead directly into the genital atrium. Near their common opening a thick muscular pouch opens into the atrium. This is the spermatheca which receives the spermatozoa from another individual, and emits them on to the ova as they pass its opening. Around the spermatheca are certain glands called the shell-glands, which also open into the atrium. The secre-

tion of these glands forms the egg-cases in which one egg and many yolk-cells are enclosed. As the egg-cases are formed they pass into two great sac-like diverticula of the atrium, one situated on each side of the body, called the uteri, i.e. "wombs." In these they are carried about by the animal for some time, but are eventually laid, and become attached to water-plants by the stickiness of their outside layer. There are two kinds of these egg-cases in *Mesostoma*, one thin-walled, called "summer eggs," and the other thick-walled, called "winter eggs." The former are believed to contain ova fertilised by the spermatozoa of the same individual; these develop rapidly, devouring the surrounding yolk-cells and the resulting young hatch out in April and May. These when they arrive at maturity cross-fertilise one another, and as a result the thick-walled capsules termed "winter eggs" are produced, which lie dormant during the winter, whilst the parent turns opaque, sinks to the bottom of the water and dies. In the spring young are hatched from the winter eggs, which produce when mature summer eggs, and in some cases are supposed after laying these to live on and produce the winter eggs of the next season; but in this respect the various species probably differ from one another.

The Turbellaria are a large group, and fall naturally into two main divisions, viz., the **Rhabdocoelida** with a rod-like gut (Gr. ῥάβδος, a staff) and the **Dendrocoelida** with a branched one (Gr. δένδρον, a tree). Each of these divisions is again subdivided; thus the order Rhabdocoelida includes the sub-orders *ACOELA*, *ALLOIOCOELA*, and *RHABDOCOELA*, whilst the Dendrocoelida are divided into *TRICLADA* and *POLYCLADA*.

To turn first to the divisions of the **Rhabdocoelida**, the sub-order *ACOELA* includes extraordinary forms in which there is no digestive cavity; the alimentary canal is represented by a porous mass of endoderm cells, amongst the interstices of which the digested food soaks. The endoderm completely fills the space surrounded by the ectoderm and muscle layers; there is no parenchyma. In almost every case there is a muscular pharynx by which the animal adheres to its prey, and through which a pseudopodium-like mass of endoderm is protruded. This protrusion secretes a solvent which disintegrates the victim, and it then engulfs the product after the manner of an *Amoeba*. In some cases, however (*Convoluta*), the endoderm is infested with small green Algae, and the animal lives largely on the compounds formed by these, needing only a scanty diet of Protozoa and Diatoms to supplement its internal provision.

The genital organs are simple; the ovary is not divided into vitellarium and germarium and no yolk-cells are produced. It has been suggested that the Acoela are the most primitive of all the phylum, and that they have been directly derived from large multinucleate Protozoa, but their development makes it possible that their peculiarities are due to degeneracy and to their association with Algae. Keeble has shown that these are sooner or later digested by the host.

The *ALLOIOCOELA* have a parenchyma and a hollow alimentary canal which has slightly developed lateral lobes. The testes are represented by scattered masses of cells without distinct ducts; and the spermatozoa apparently find their way to the main vasa deferentia by passing through the interstices of the parenchyma. The germaria are two in number and have long ducts opening into the genital atrium distinct from those of the vitellaria.

The *RHABDOCOELA* are the most highly developed forms of the Rhabdocoelida; their alimentary canal is cylindrical and surrounded by a mass of extremely watery parenchyma which simulates a body cavity. The arrangement of the genital organs has been described above.

The first division of the **Dendrocoelida**, the *TRICLADA* (Gr. τρι-, triple, κλάδος, a branch), derive their name from the circumstance that there are three main branches of the alimentary canal, one in the middle line running forward from the inner end of the pharynx, and one running backwards at each side of the pharynx. There are a pair of germaria formed from the most anterior branches of the great lobed ovaries; they discharge into the same ducts as the vitellaria. The uterus is an unpaired sac. The group includes marine, fresh-water and terrestrial forms. *Planaria* (*Dendrocoelum*) is a common form in the streams of both Britain and Canada.

The *POLYCLADA* are a marine group and are thought by some authorities to be the most primitive of all Turbellaria. Their name is suggested by the fact that the alimentary canal consists of many branches radiating from a central stomach into which the large pharynx opens. The ovary is a lobed organ not divided into vitellarium and germarium. The eggs are laid in capsules which contain only one or two; these capsules are arranged in plate-like masses bound together by slime. They develop into free-swimming young known as Müller's larvae. These are little oval organisms provided with a ciliated band drawn out into eight longitudinal loops, and on these the cilia are arranged in transverse rows

fused at the base so as to resemble the combs of the Ctenophora. The resemblance of these ciliated loops to the "ribs" of the Ctenophora suggested to Lang the idea that Turbellaria were Ctenophora which had become adapted to a creeping life, in which a marked bilateral symmetry had replaced the generally radial arrangement of the organs of the normal Ctenophora, though traces of the latter arrangement remain in the Polyclada. The brain on this view would be the apical plate which had shifted forward; the stomach with its radiating branches would correspond to the funnel of the Ctenophora and the canals in connection therewith; the pharynx sheath would represent the stomodaeum, the so-called "stomach" of the Ctenophora; but the eversible pharynx, the accessory genital organs, i.e. genital ducts, penis, bursa copulatrix, uteri, etc., and above all the excretory system must be regarded as new acquisitions. This view, which at first was not received with much favour, has

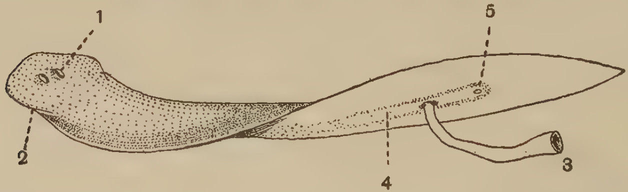


FIG. 42. *Planaria polychroa* × about 4.

1. Eye. 2. Ciliated slit at side of head. 3. Mouth of proboscis. 4. Outline of the pharynx sheath into which the pharynx can be withdrawn. 5. Reproductive pore.

received strong support by the investigation of a marine organism known as *Ctenoplana*. This is a flattened animal resembling a Polyclade in shape and in the circumstance that the ventral surface is covered with cilia with which it creeps. It possesses however an apical plate of thickened nervous ectoderm supporting a mass of otoliths on bars of fused cilia, and there are eight short "ribs" radiating from this plate. These ribs as in Ctenophora are thickened bands of ectoderm bearing combs of cilia fused at the base. The funnel and its canals are represented by a lobed alimentary canal, continued on each side into a tentacle canal, from the end of which springs a long retractile tentacle. The genital organs have their independent ducts opening directly to the exterior. In all these respects therefore *Ctenoplana* is intermediate between the Polyclada and the Ctenophora. The evolution of the more complicated systems of genital organs amongst the Turbellaria out of the simpler

arrangement in the Polyclada, has probably been the result of laying the eggs in numbers surrounded by a capsule. This led to a struggle amongst the eggs, resulting in the sacrifice of the smaller to the needs of the larger ova, and this to the production of weak ova to serve as food for the others, with the consequent differentiation of the ovary into germarium and vitellarium.

Class II. Trematoda.

The remaining two groups of Platyhelminths have taken to a parasitic mode of life and this has to a great extent influenced their organisation. The term parasite is applied to an animal which lives on the external surface of or in the interior of another animal, termed the host, and nourishes itself at the host's expense. If the infesting organism like the Algae in *Convoluta* is made use of by the host, the relation between the two is designated symbiosis. If however the infesting animal only makes use of its host's body as shelter and nourishes itself from the fragments of the host's food, the relation between the two is referred to as commensalism. The Trematodes have lost the external ciliation of the skin, the ectoderm being everywhere covered with cuticle. In other features of their anatomy they present a great resemblance to the Triclade Turbellaria, and one family, the Temnocephalidae, may be described as intermediate between the two classes of Platyhelminths, since its members still retain patches of ciliated skin. For the most part they live on or in the bodies of Vertebrates, attaching themselves either to the skin or to the alimentary canal or its outgrowths.

One of the most characteristic features of Trematoda is to be found in the suckers by which they adhere to their prey. Often indeed the lips of the mouth are thickened and muscular so as to constitute an oral sucker, but there is always a ventral adhesive disc provided with suckers or hooks or both. The mouth is situated at or near the anterior end of the body; it leads into an oral funnel opening into a muscular pharynx, which by alternate expansion and contraction pumps in the juices of the prey. Its action is thus different from that of the pharynx of Turbellaria, which, as we have seen, can act as a protrusible sucker. Behind the pharynx the alimentary canal divides into two parallel forks running back to the posterior end of the body, and beset with branches which in some cases may unite with one another across the middle line. It thus resembles what the alimentary canal of a Triclade would become were the mouth shifted to the anterior end

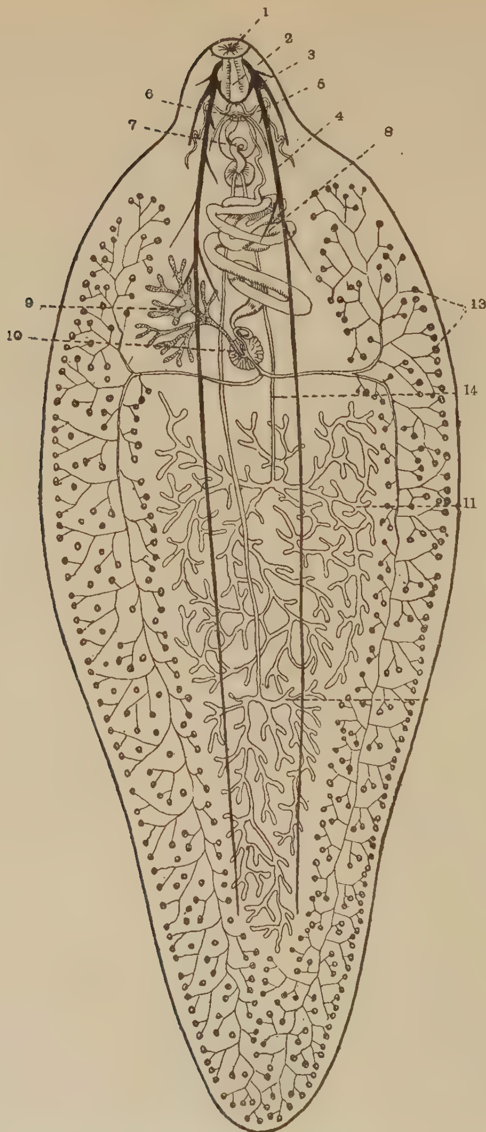


FIG. 43. Diagram of reproductive and nervous system of *Distomum hepaticum* × about 8. From Leuckart.

1. Mouth. 2. Pharynx. 3. Nerve-ring. 4. Chief longitudinal nerve. 5. Beginning of alimentary canal. 6. Opening of penis. 7. Vesicula seminalis. 8. Uterus. 9. Ovary. 10. Shell-gland. 11. Anterior testis. 12. Posterior testis. 13. Yolk-glands. 14. Vas deferens.

of the body. The nervous system is remarkable for the fact that several trunks of equal size are given off from each side of the brain. The reproductive organs resemble those of a Rhabdocoele like *Mesostoma*; thus the germarium is developed only on one ovary, of which it is a basal branch, and the testes each consist of a lobed organ directly continuous with the vas deferens. The main peculiarities are as follows: there is no spermatheca; the spermatozoa from another individual enter either by a dorsal pore or two lateral pores, leading into a canal or canals which join the oviducts where they unite with one another. These ducts, totally unrepresented in Turbellaria, are called the "canals of Laurer." Further, the genital atrium is situated on the anterior part of the body in front of the ventral sucker. There is no uterus comparable with that of Turbellaria; the so-called uterus being a long coiled tube composed of the conjoined oviducts (vitellarian ducts). Finally the testes are so large that there is not room for them side by side, but in order to stow them away one is situated behind the other.

Trematoda are divided into two orders called respectively the *MONOGENEA* and the *DIGENEA*. In the first named the egg gives rise to a larva which develops continuously into the adult; the main organ of adhesion is a disc situated at the posterior end of the body and armed with suckers or hooks, usually both, and there are two lateral vaginae from which the canals of Laurer lead inwards. The excretory system opens by two dorsal pores. One of the commonest of the Monogenea is *Polystomum integerrimum*, found in the bladder of the Frog. This animal has an adhesive disc bearing six suckers. The fertilised egg of *Polystomum* is discharged through the cloaca of the Frog into the water. After some time a larva hatches out which has a forked alimentary canal, but which is without genital organs and has no suckers, although the posterior adhesive disc is clearly differentiated. It is provided with a number of transverse bands of cilia by means of which it swims about until it finds a tadpole, to the skin of which it attaches itself. It creeps into the branchial chamber of its host and loses its cilia, and commences to develop genital organs and suckers. About the time of the tadpole's metamorphosis the Trematode wanders down the alimentary canal into the bladder. *Sphyranura osleri* is an allied form parasitic on the skin of the Urodele *Necturus*. Its posterior disc carries two large suckers and two hooks.

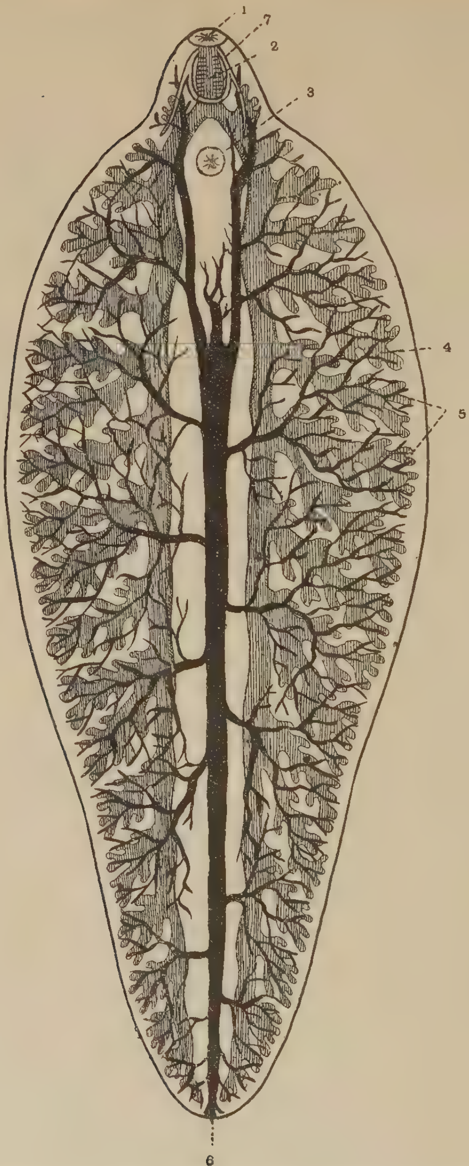


FIG. 44. Diagram of digestive and excretory system of *Distomum hepaticum* × about 8. From Leuckart.

1. Mouth. 2. Pharynx. 3. Reproductive pore. 4. Branch of alimentary canal. 5. Branches of excretory system. 6. External opening of excretory system. 7. Nerve-ring.

The *Digenea* commence life as larvae which become parasitic in some animal, where they give rise by gemmation to several generations of secondary larvae, which develop into adult forms only when they are swallowed by a second animal. The life-history therefore includes an alternation of generations and is only completed in two hosts. The Digenea further differ from the Monogenea in having as main adhesive organ a sucker situated on the anterior part of the ventral surface, in having only a single "canal of Laurer" which opens on the dorsal surface, and finally in the fact that the main trunks of the excretory system or in other words the tubes of the two branched nephridia coalesce to form a single trunk which opens to the exterior by a median posterior pore. The Liver-fluke, *Distomum hepaticum*, is an example of the Digenea; it is parasitic in the liver and bile-ducts of the sheep, causing a wasting disease called sheep-rot. It gives rise to a larva consisting of a solid mass of cells, the outermost layer of which is ciliated. This larva cannot survive unless it reaches a pond-snail of the species *Limnaea truncatula*. In the pulmonary chamber of this animal it loses its cilia, enlarges and becomes hollow, forming a structure called the sporocyst, which sometimes divides into two or more. Germ cells are budded off from the wall of the sporocyst into its cavity. These by division form masses which develop into secondary larvae called rediae, which are provided with a muscular pharynx and a sac-like alimentary canal. These larvae have a pair of blunt processes on the under side near the posterior end, by the aid of which they move. They force their way out of the sporocyst and enter the tissues of the snail, being found especially in the liver. From the inner surface of their body-wall germ cells are budded off which give rise to other rediae, which escape from the parent by an opening near the anterior end. After a time the rediae give rise to larvae of a third kind called cercariae. These have suckers like the adult, and a forked alimentary canal with a pharynx; they are provided with a tail stiffened by a rod of gelatinous tissue recalling the Vertebrate notochord. By the aid of the tail they work their way out of the snail and attach themselves to blades of grass. The tail then falls off and they enclose themselves in a cyst of mucus, and remain there till they are eaten by a sheep, from whose intestine they pass into its liver, where they develop genital organs and become mature.

Class III. Cestoda.

The Cestoda are sharply distinguished from the two preceding classes of Platyhelminthes by the total absence of an alimentary canal. They are all internal parasites, living in the alimentary canal of their hosts, and absorb the half-digested juices of their hosts through all parts of their skin.

As in Trematoda, there is a well-marked cuticle which protects the animal from the action of the digestive juice of the host. The ectoderm has undergone an extraordinary modification. Its cells have become long and filamentous, since they have acquired long narrow necks, and the body of the cell with the nucleus has been pushed downwards into the subjacent tissues. These necks are however of very various lengths, and so the ectoderm, although fundamentally a single layer of cells, presents the appearance of a thick band of many layers of nuclei. The ectoderm cells intermixed with longitudinal muscles form the outer or as it is termed the cortical zone of the animal. Inside this and surrounded by the circular muscles is the central mass of parenchyma, which is termed the medullary zone (Lat. *medulla*, pith) in which the genital organs and the excretory and nervous systems are embedded. Many of the cells of the parenchyma secrete calcareous matter and form the so-called calcareous corpuscles.

Each portion of the body of a Cestode which contains a set of reproductive organs is called a proglottis, and is budded off from the anterior portion which is called the head[1]. The latter is provided with suckers, and generally, in addition, with a circle of hooks situated on a prominence called the rostellum (1, Fig. 45, B). With the head the Cestode adheres to its host; its hinder part or neck buds off proglottides in which new sets of reproductive organs are formed, and this process is repeated an indefinite number of times so that a chain of proglottides is formed. The oldest proglottis is thus the hindermost. This method of segmentation is called strobilisation on account of its resemblance to the formation of the Ephyrae by a Hydra-tuba (p. 78); it differs from the segmentation of the Annelida, where the new segments arise not in the neck but in the tail.

The excretory system consists of a larger and a smaller trunk on each side, which unite in the last proglottis to end in a

[1] Some authorities regard the so-called "head" as the most posterior portion of the animal.

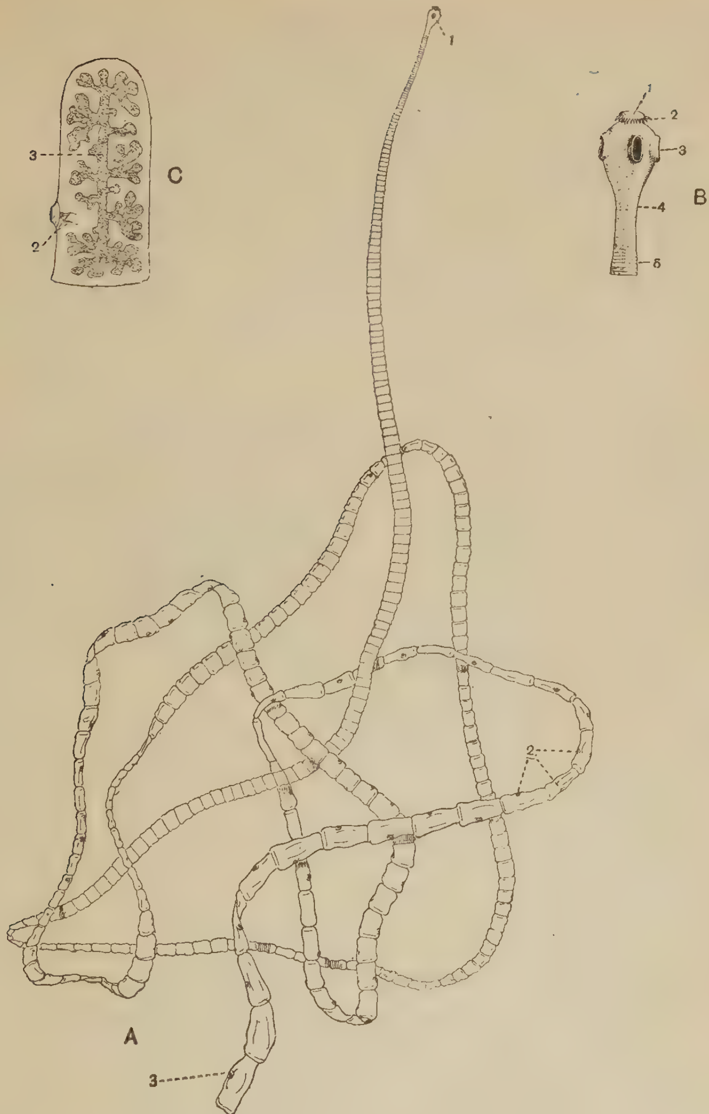


FIG. 45. *Taenia solium*. Slightly magnified.

A. Entire worm showing head and proglottides. 1. Sucker on head. 2. Genital pores. 3. Ripe proglottis.
B. Head. 1. Rostellum. 2. Hooks. 3. Suckers. 4. Neck. 5. Commencement of strobilisation.
C. Ripe proglottis broken off from worm. 2. Remains of vas deferens and oviduct. 3. Branched uterus crowded with eggs.

contractile vesicle opening by a median posterior pore. In each proglottis the trunks on each side are connected with their fellows on the opposite side by transverse canals. The nervous system consists of a ring in the head, whence two lateral trunks arise. There is no brain—the impressions the animal receives from the outside world being few and simple.

The reproductive organs have the same general structure as those of the Trematoda. The vitellarium is however often unpaired, whereas there are usually a pair of germaria. There is a large uterus (8, Fig. 47) which appears to be a lateral outgrowth from the conjoined oviducts. From the circumstance that in primitive Cestoda this uterus opens to the exterior independently

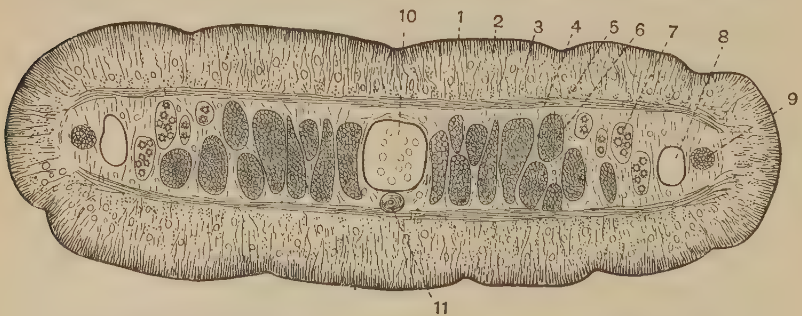


Fig. 46. Transverse section through a mature proglottis of *Taenia* × about 12.

1. Cuticle. 2. Long-necked cells of ectoderm. 3. Longitudinal muscle fibres cut across. 4. Layer of circular muscles. 5. Split in the parenchyma which lodges a calcareous corpuscle. 6. Ovary. 7. Testis with masses of male germ-cells forming spermatozoa. 8. Longitudinal excretory canal. 9. Longitudinal nerve-cord. 10. Uterus. 11. Oviduct.

of the genital atrium it is believed that it corresponds to the canal of Laurer in the Digenetic Trematoda. If this be so the functions of the genital atrium and Laurer's canal have been exchanged in Cestoda, for in Trematoda the atrium permits eggs to escape whilst Laurer's canal admits spermatozoa from another individual, in Cestoda these spermatozoa enter through the atrium whilst the canal is enlarged to form a uterus. The testes are in Cestoda represented by a multitude of small rounded bodies (7, Fig. 46, 9, Fig. 47) from which excessively fine ducts are given off which unite to form the single vas deferens ending in the penis. As the proglottis gets older the eggs all pass into the uterus, which swells enormously, displacing and destroying the other organs. In this condition the proglottis drops off. This process is continually being

repeated so that a single parasite keeps on casting off portion after portion, each charged with ova capable of developing. In this way a Cestode firmly lodged in the alimentary canal of its host can produce an almost indefinite number of eggs.

In the more primitive Cestoda the egg-cases, which as in Trematoda contain an ovum and a multitude of yolk-cells, escape from the detached proglottis through the opening of the uterus into water. In a short time a larva hatches out, consisting of an outer layer of ciliated cells surrounding a solid internal mass which develops six chitinous hooks. After swimming in the water for a short time the larva is swallowed by an aquatic animal, loses its outer

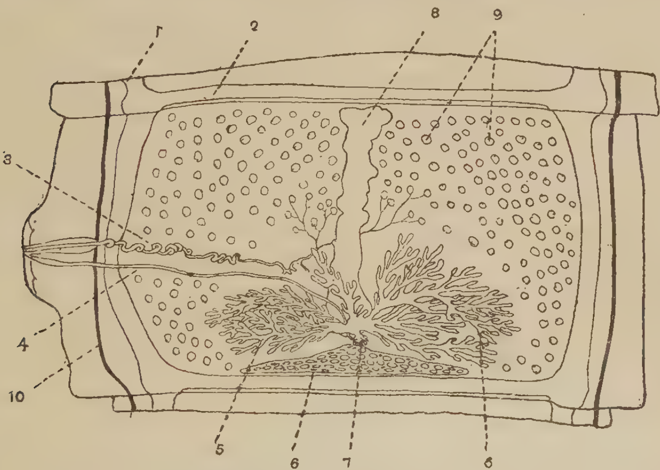


FIG. 47. Diagram of a ripe proglottis of *Taenia solium*. From Cholodkowsky × about 10.

1. Longitudinal water-vascular canal. 2. Transverse water-vascular canal. 3. Vas deferens. 4. Vagina. 5. Ovary. 6. Yolk-gland. 7. Shell-gland. 8. Uterus. 9. Testes. 10. Longitudinal nerve.

layer of cells, thus exposing the hooks and becoming what is now termed an onchosphere. In the more modified Cestoda the uterus has no external opening, and the eggs escape from the proglottis only by decay. The remains of the proglottis, including the eggs, are swallowed by some animal, and soon after an onchosphere hatches out, no cilia being formed. In every case the onchosphere bores through the alimentary canal of its host, and is carried by the blood-stream to a suitable spot in the tissues where it fixes itself. Once fixed, the larva increases very much in size and generally becomes hollow so as to resemble a bladder. An infolding or

invagination of part of the outer layer now takes place, forming a pouch, on the inner side of which the suckers and hooks of the adult head make their appearance. The pouch is then turned inside out and a well-marked head is thus formed. The larva is now known as a bladder-worm or Cysticercoid and is found parasitic in a great number of animals. A very common form is *Cysticercus pisiformis* found in the coelom of the Rabbit attached to the mesentery (see p. 437). *Coenurus cerebralis* is a dangerous Cysticercoid in which the bladder can become as large as a plum and on which not one but numerous heads are formed. It is found lodged in the brain of the Sheep and other domestic animals and causes the disease known as gid or staggers. A still more dangerous form is *Echinococcus polymorphus*, in which the bladder may become as large as a man's head. This enormous vesicle buds off from its inner surface secondary vesicles on each of which numerous heads are formed. This parasite is found in the Pig, Sheep, and even Man, in the liver and other internal organs.

The Cysticercoid can complete its development only when its first host is eaten by another animal. Then the bladder is cast off whilst the head firmly attaches itself by its hooks and suckers to the alimentary canal of its new host and commences to bud off proglottides. Though the adult may attain an immense length (as much as 20 feet) it is a much less dangerous parasite than the larva, and rarely produces worse symptoms than giddiness and a certain amount of abdominal pain. The adults are found chiefly in carnivorous animals, above all in the Dog, Wolf and allied species. Thus *Cysticercus pisiformis* becomes *Taenia serrata*, *Coenurus cerebralis* gives rise to *Taenia coenurus*, and *Echinococcus polymorphus* to *Taenia echinococcus*, all three infesting the alimentary canal of the Dog and its allies. The common *Taenia solium* found in the human intestine is developed from a Cysticercoid found in the muscles of the Pig.

Bothriocephalus latus, which may attain a length of 30 feet, is the largest Cestode found in Man. It belongs to a more primitive division of the class than *Taenia*, for it gives rise to a free-swimming ciliated larva, described above, which is swallowed by the Pike or the Perch. In this it develops into a solid larva termed a Plerocercoid which gives rise to the adult when the fish is eaten by Man.

It is obvious that an animal which like a Digenetic Trematode or a Cestode depends for its survival on such a combination of

lucky chances as that of transference from one particular species of animal to another animal of a definite kind must develop large powers of reproduction. In the Trematode this is chiefly manifested in the power of the larva to reproduce itself asexually, but in the Cestoda the power is in most cases only developed when the animal is in the adult condition. Considerable discussion has taken place as to whether the process of strobilisation is, or is not to be regarded as a production of new individuals. When we recollect that the separated proglottides often retain life for some time after being cast out of their host, it would seem that there was much to be said in favour of regarding them as sexual individuals and the head as an asexual one. The most probable view on the whole is that of Lang, who suggests that in the ancestor of modern Cestoda the hinder part of the body which contained the genital organs was separated at maturity, as occurs in the case of some Polychaeta. When the Cestode took to living in the alimentary canals of Vertebrata, the abundant food supply and favourable temperature stimulated the powers of regeneration so that the missing part was quickly reproduced, and by the hurrying on of this process of regeneration the process of strobilisation was evolved, exactly as occurred in the Scyphistoma of *Aurelia*. It is interesting to notice that *Archigetes*, found mature in the coelom of the Oligochaet worm *Tubifex*, is the only Cestode which completes its development elsewhere than in a Vertebrate, and in this case only one proglottis is produced, which never separates from the head. To the posterior end of this proglottis an appendage is attached representing the bladder of the Cysticercoid, in which the six hooks of the onchosphere still remain embedded.

The Platyhelminthes are classified as follows:

Class I. Turbellaria.

Platyhelminthes with soft, usually leaf-like bodies and a ciliated ectoderm: rhabdites are often present: free-living.

Order 1. **Rhabdocoelida.**

Turbellaria with a straight, rod-like alimentary canal and a protrusible pharynx

Sub-order 1. **Acoela.**

The digestive system is represented by a mass of endoderm cells which contains no cavity: a short pharynx and single otocyst are present.

Sub-order 2. **Alloiocoela.**

The alimentary canal is lobed: the testes are scattered.

Sub-order 3. **Rhabdocoela.**

The alimentary canal is rod-shaped, the testes are compact lobed organs.

Order 2. **Dendrocoelida.**

Turbellaria with a branched alimentary canal.

Sub-order 1. **Triclada.**

The alimentary canal has three main branches, one running forward and two running back. Male and female openings united.

Sub-order 2. **Polyclada.**

The alimentary canal has many branches sometimes uniting with one another in a net-like manner, i.e. "anastomosing." Male and female openings as a rule distinct. Marine.

Class II. Trematoda.

Parasitic Platyhelminthes with usually leaf-like, rarely cylindrical bodies: no cilia on ectoderm: forked alimentary canal: ventral sucker or suckers and hooks often present: not segmented.

Order 1. **Monogenea.**

Trematodes with a sucker or suckers at the posterior end and in some cases another anteriorly. Often external parasites or infesting the mouth, nose or branchial cavities of their hosts. Development direct.

Order 2. **Digenea.**

Trematodes with a sucker at the anterior end and another on the ventral surface or posteriorly. Internal parasites and their organs of adhesion more weakly developed than in the Monogenea. Development with an alternation of generations.

Class III. Cestoda.

Parasitic Platyhelminthes with elongated and usually segmented body: no mouth or alimentary canal: suckers and hooks present but on the head only: the segments break off when ripe.

CHAPTER VI

PHYLUM NEMERTINEA

The Nemertines belong to that category of animals popularly styled "worms"; that is to say they are long, soft-bodied animals, without limbs or appendages of any kind, which progress by undulatory movements of the body. Most Nemertines are marine, living under stones and amongst seaweed; a few are found in fresh water and one or two species are terrestrial.

They swim in a graceful, undulating fashion, but they are much more sluggish in their movements than Annelida. It is a common and characteristic sight to see an isolated contraction passing slowly back along the body. Some species are minute, others, e.g. *Lineus marinus*, attain a length approaching 100 ft., and are perhaps the longest animals known.

The ectoderm consists of long, narrow, ciliated cells. In this they resemble the Turbellaria, but they differ from the latter animals profoundly in the structure of the alimentary canal. This canal is it is true straight and unbranched, but it differs from the alimentary canal of all Coelenterata and of Platyhelminthes in possessing two openings—one in front, the mouth, for taking in food, and one behind, the anus, for rejecting undigested material. For most of its course the alimentary canal is sacculated; that is to say, it is produced at the sides into a series of short broad pouches; otherwise it is not differentiated in any way.

The most characteristic organ of the Nemertine is the proboscis. This is a long tube lying above the alimentary canal, ending blindly behind, and opening to the exterior in front. The proboscis is a part of the outer skin invaginated, and when retracted it is surrounded by a closed space lined by a well-defined epithelium called the proboscis-sheath. This space contains a watery fluid, and its wall beneath the epithelium possesses powerful circular muscles. When these contract the proboscis is partially forced out of the sheath by being turned inside out and consequently

protruding from the front end of the body at the same time. It can never be completely turned inside out, for certain cords traversing the proboscis-sheath restrain it. At the point in its wall which is at the anterior end when the process of turning inside out has reached its utmost limits, there is in the higher Nemertines a short lateral pouch in which a horny spike, the stylet, is secreted. Round the base of this open poison-glands, so it can be seen that the proboscis is an offensive organ for seizing prey. So far as we know all Nemertines are carnivorous. Amongst the lower Nemertines the stylet is not developed, nevertheless the proboscis can be employed to catch prey; it is quickly thrust out and coiled spirally round the victim and then retracted so as to push the prey into the mouth. This retraction is brought about by a muscular band which attaches the end of the proboscis to the sheath. The land Nemertines (*Geonemertes*) are said to travel by thrusting out the proboscis, attaching it to foreign objects and drawing up the body after it.

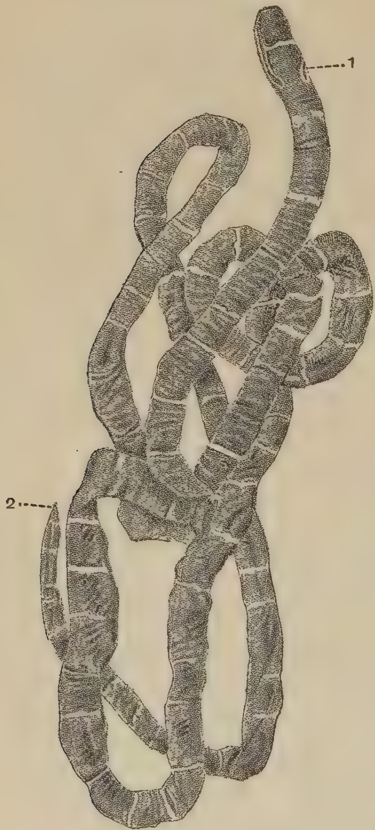


FIG. 48. *Lineus geniculatus* × $\frac{3}{4}$.
1. Lateral slits on head. 2. Anus.

Underneath the ciliated ectoderm of Nemertines there is a series of powerful circular and longitudinal muscles: these layers are continued, but in the reverse order, on to the walls of the proboscis, since this is only invaginated skin. Under extreme irritation the extended proboscis is sometimes torn from the body—by the heightened pressure of the fluid in the sheath—and in one instance such a disjoined proboscis was mistaken on account of its active contractions for a new species of Nemertine.

There is a well-defined central nervous system amongst Nemertines, consisting of a pair of ganglia lying at the front of and above the mouth—less frequently at the sides of it—and connected by a nervous band or commissure which passes above the proboscis-sheath. The hinder parts of the ganglia are more or less distinctly separated as posterior lobes, and come into close relation with curious pouches of invaginated ectoderm, termed cephalic pits (Fig. 49), which seem in some cases at any rate to subserve the respiration of the nervous tissue, for the latter in some species contains haemoglobin. The ganglia are continued backwards into two powerful nerve-cords lying at the sides of the body. In the lower species these cords can be seen to lie just beneath the ectoderm and to be but thicker portions of a sheath of nerve-fibrils extending all round the body, and derived from the bases of the ectoderm cells. In the higher species the nerve-cords lie well within the muscles, and this sheath is not so evident. The principal resemblance between Platyhelminthes and Nemertinea lies in the arrangement of these ganglia and lateral nerve-cords.

Sense-organs in the form of eyes of simple structure often occur immediately over the region of the ganglia.

The interstices between the various organs inside the muscles are filled up with parenchyma like that of Platyhelminthes, but there exist three longitudinal tubes with well-defined walls which are regarded as blood-vessels. Two of these tubes lie at the sides of the alimentary canal, and one is situated above it and below the proboscis-sheath. These vessels are connected anteriorly by arches and they unite with one another in both the head and tail. These blood-vessels are to be regarded as last remnants of the cavity which in the embryo intervenes between ectoderm and endoderm, which in Coelenterata is filled with almost fluid jelly (containing in *Aurelia* 99 °/ₒ of water). This cavity is called by various names. By embryologists it is termed the blastocoele or segmentation cavity, because it appears early in development by the mutual separation of the blastomeres or first cells resulting from the division of the fertilised egg. By students of adult anatomy it is termed haemocoele (Gr. αἷμα, blood) because the fluid which it contains is the first form of blood, but the best and simplest name for it is one coined in Germany, viz. primary body-cavity.

The excretory organs have the form of a pair of branched nephridia opening at the sides of the body not far behind the cephalic pits. Their branches end blindly and the terminations

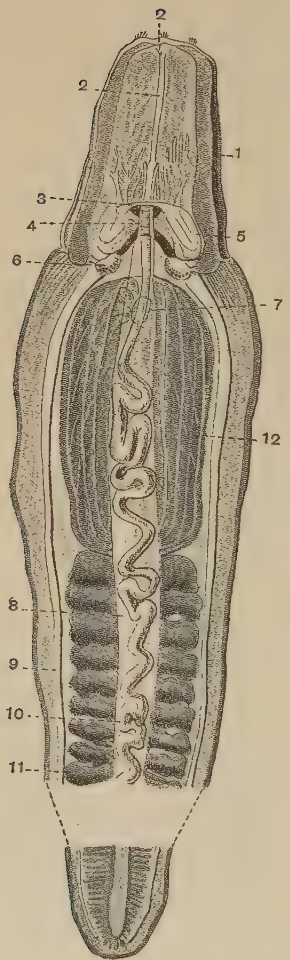


FIG. 49. *Cerebratulus fuscus.* Young transparent form × 7. After Bürger.

1. Cephalic pits. 2. Opening leading into the retracted proboscis. 3. Dorsal commissure of nervous system. 4. Ventral commissure. 5. Brain. 6. Posterior lobe of brain which comes into connection with the cephalic pit. 7. Mouth. 8. Proboscis sheath. 9. Lateral vessel. 10. Proboscis. 11. Pouches of alimentary canal. 12. Stomach.

of these are closely applied to and even indent the wall of the lateral blood-vessel, while in each termination there is a tuft of cilia.

The Nemertinea have testes and ovaries borne by different individuals, that is to say the sexes are separated. The generative organs are exceedingly simple, consisting in both sexes of packets of cells situated along the sides of the body alternating with the pouches of the alimentary canal. No permanent genital ducts exist, but when the ova and spermatozoa are ripe they appear to make temporary ducts for themselves. The egg develops in many cases into a remarkable larva called a Pilidium. This is shaped something like a policeman's helmet with ear lappets. The edge of the helmet, including the lappets, is fringed with powerful cilia, and there is besides a tuft of long cilia at the apex. Underneath the helmet is the opening of the mouth, which leads into a sac-like gut devoid of an anus.

The adult is developed from the Pilidium in an extraordinary way. Four invaginations of ectoderm appear on the under side of the larva, at the sides of the alimentary canal. These grow both upwards and inwards until they completely surround the canal. The inner walls of the pockets form the ectoderm of the adult. When the process is complete the alimentary canal surrounded by the new ectoderm drops out of the Pilidium and forms the Nemertine.

Many species of Nemertine are found on the British coast. As examples we may mention *Lineus* (Fig. 48), a long thin form without a stylet in the proboscis, and *Tetrastemma*, a short broad form with four eyes and a stylet in the proboscis. A remarkable land Nemertine *Geonemertes* is found in Australia. It moves by ejecting the proboscis coiling it round a twig and then pulling the rest of the body after it.

The Nemertines, so far as our present knowledge extends, form a completely isolated group in the animal kingdom.

From the circumstances that some Rhabdocoel Turbellarians have a protrusible organ in the anterior part of the body, and that the excretory organs of Nemertines bear a certain resemblance to those of Platyhelminthes, it has been supposed that Nemertines and Platyhelminthes are allied. The presence of an anus in Nemertines tells strongly against this view, since the change from a single opening to the alimentary canal to two openings, one for ingestion of food and one for rejection of faeces, was a momentous step in evolution and must have required a long period for its completion. The absence of all accessory genital organs in Nemertinea as contrasted with their presence and elaboration in Platyhelminthes tells very strongly against the mutual affinity of the two groups.

The Nemertinea are divided into classes in accordance with the condition of the nervous system and the arrangement of the layers of muscles in the skin. These classes are as follow:

Class I. Protonemertini.

A nervous sheath underlies the entire ectoderm; the lateral nerve-cords are mere thickenings of this sheath, and are situated outside the layers of muscles: no stylet in the proboscis.

Ex. *Carinella.*

Class II. Mesonemertini.

A nervous sheath underlies the entire ectoderm; the lateral nerve-cords are more deeply situated, lying between the outer circular and the inner longitudinal muscles: no stylet in the proboscis.

Ex. *Cephalothrix.*

Class III. Heteronemertini.

A nervous sheath surrounds the body. Both it and the nerve-cords lie inside a special layer of longitudinal muscles,

which are derivatives of the ectoderm cells, but outside all the other muscles : no stylet in the proboscis.

Ex. *Lineus*, *Cerebratulus*.

Class IV. Metanemertini.

No nervous sheath but definite peripheral nerves : the lateral nerve-cords lie within all the muscle layers : the proboscis is armed with a stylet.

Ex. *Tetrastemma*, *Geonemertes*, *Malacobdella*.

Classes I—III are often united as the Class *Anopla*, characterised by the absence of a stylet in the proboscis. Class IV is sometimes termed *Enopla* (i.e. armed) to contrast it with the remaining Nemertines or Anopla.

CHAPTER VII

PHYLUM ROTIFERA

THE Rotifera are minute animals mostly confined to fresh water, a few only being found in the sea. Many of them swim about by means of a loop of cilia which encircles the front end of the body, but some are sessile. The motion of these cilia induced the early observers to think that the animal had wheels in front, whence the name (Lat. *rota*, a wheel; *fero*, to carry). There is a complete transparent alimentary tube, ending in an anus situated on the dorsal side in front of the hind end of the body, the latter forming a ventral projection called the foot. The first part of the tube is a stomodaeum, and lined like the rest of the skin with cuticle. This cuticle is thickened to form teeth which work on one another, the whole organ being called a mastax. The activity of the mastax enables one at once to distinguish a Rotifer from other minute animals.

Floscularia cornuta, often termed *F. appendiculata*, is a widely distributed species. It lives in ponds, ditches and pools, usually attached by its posterior end to some water-weed or other body and surrounded by a gelatinous tube into which the animal can retire. The length of the animal when extended is 0·2 to 0·3 mm. The body is covered by a thin cuticle, and may be divided into three regions, the head, the trunk and the foot. When the animal is extended the last-named is stretched out and smooth, but it is wrinkled when the animal withdraws into its tube. It terminates in a disc, on which opens the duct of two large glands which secrete an adhesive substance, by means of which the foot is anchored.

The anterior end of a Rotifer, on which the mouth opens, is called the disc. In *Floscularia* this is produced into five long tentacle-like processes fringed with stiff bristles which serve as a net to entangle small animals and plants. The cilia which produce

the current by means of which the prey is captured are situated inside the ring of tentacles. They take the form of a horseshoe-shaped band open dorsally, the mouth being situated in the centre

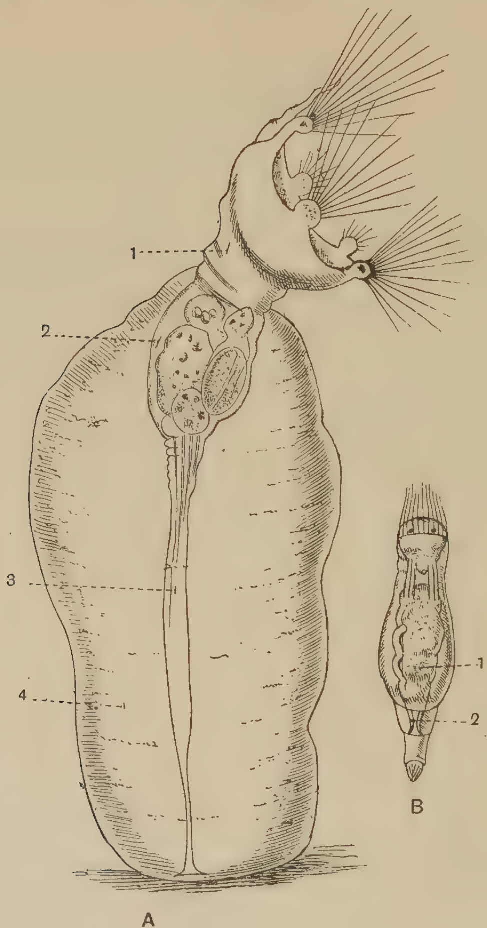


Fig. 50.

A. *Floscularia cornuta.* Female magnified. From Hudson. 1. Head. 2. Trunk. 3. Foot. 4. Gelatinous tube in which the animal lives.

B. *F. campanulata.* Male magnified. 1. Vesicula seminalis. 2. Penis.

of the horseshoe. This band of cilia is termed the velum: in other Rotifera it is a complete circle but is folded back on itself in such a way that a loop is produced which lies dorsal to the mouth.

This loop is called the trochus; it usually consists of more powerful cilia than the rest of the velum, which is termed the cingulum. The groove between the two bands in which the mouth lies is covered with fine cilia. In the genus *Rotifer* the trochus is composed of two almost circular lobes, which were described as wheels by the first naturalist who observed them, and this circumstance, as we have said, suggested the name given to the genus and afterwards bestowed on the whole phylum.

Within the cuticle which covers the body is the ectoderm. This takes the form of a protoplasmic layer with scattered nuclei, showing no cell-outlines. It surrounds a spacious primary body-cavity, which contains a fluid with no amoebocytes; in this float the various organs of the body connected more or less closely together by connective tissue-cells. Connective tissue is the name given to a tissue like the parenchyma of Platyhelminthes and Nemertinea, consisting of stellate cells united to one another by their processes, but in which, along the outer margins of these united cells, tough fibres are secreted which cross one another and give firmness and tensile power to the whole. Fibres are very scantily developed in the connective tissue of Rotifera. The cuticle of the ectoderm is the most important part of the skeleton. The muscles do not form a continuous layer underneath the ectoderm as is the case with the Platyhelminthes and the Nemertinea but consist

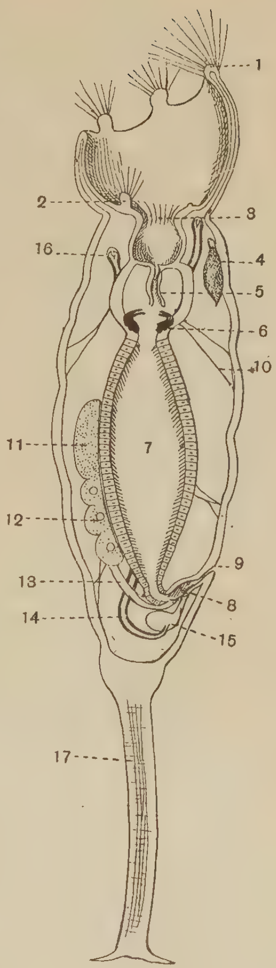


Fig. 51. Diagram of *Floscularia*.

1. Circle of tentacles bearing bristles. 2. Velum. 3. Mouth leading to vestibule. 4. Brain. 5. Oesophagus hanging like a funnel into the crop. 6. Mastax with trophi. 7. Stomach. 8. Rectum. 9. Opening of cloaca. 10. Strands of muscles. 11. Yolk-gland part of ovary. 12. Ovarian part of ovary. 13. Oviduct. 14. Excretory duct opening into 15, urinary bladder. 16. A tag with a tuft of cilia. 17. Longitudinal and circular muscles in foot.

of isolated bands, chiefly longitudinal, which retract the disc and the foot and bend the body in various ways, the recovery of its original shape being due largely to the elasticity of the cuticle.

The food, which consists of Protozoa and other small organisms, is swept into the mouth by the action of the surrounding cilia. The mouth leads through a wide vestibule into an oesophagus, which is ciliated and projects down into the so-called gizzard or mastax which, next to the ciliary rings on the head, is the most characteristic organ of a Rotifer. The vestibule, oesophagus and mastax are all part of the stomodaeum. The cuticle lining the mastax is thickened so as to produce the trophi, which are hard, chitinous, chewing organs; of these there are typically three, two mallei and an incus on which they strike. The incus, a **Y**-shaped piece, consists of two rami and a central piece or fulcrum. Each malleus is composed of a manubrium and an uncus or head, which may be toothed. The shape and arrangement of these hard parts is of great value in classification. In some species the mallei are absent altogether, and the two rami of the incus then work against one another like two lateral teeth. In the NOTOMMATIDAE the mallei can be protruded through the mouth and are used to cut into the cells of Algae on which the animals browse. In *Floscularia* and its allies there is a dilatation of the stomodaeum, called the crop, interposed between the mastax and the oesophagus, and the latter hangs down into the crop just as a funnel might hang into a tumbler: the crop can be everted through the mouth.

After passing between the jaws the food enters the stomach, which is lined with cilia; here the food loses its original colour and becomes tinged with the brown secretion of the walls of the stomach. In most forms two salivary glands open into the mastax and two gastric glands into the stomach, but these have not been clearly made out in *Floscularia.* The stomach is separated by a constriction from the ciliated rectum, and this ends in a non-ciliated tube into which the genital and excretory organs also open. This tube consists of ectoderm turned in at the anus and is therefore termed the proctodaeum (Gr. πρωκτός, anus), a word formed on the analogy of stomodaeum. The alimentary canal of Rotifera, like that of the lower Vertebrata, thus terminates in a cloaca, that is to say in a tube which is a common channel for all the products which have to be expelled from the body. The word cloaca it is hardly necessary to remind the reader was originally applied to the great main sewer of ancient Rome.

The excretory system consists of two longitudinal ducts consisting of columns of perforated cells, which bear a number of small tags hanging freely into the body-cavity (Fig. 52), i.e. of two long nephridia beset with short branches terminating in solenocytes each containing a cavity in which a bundle of flagella wave slowly about. In *Floscularia* four or five pairs of solenocytes have been seen. The longitudinal ducts are usually connected by a transverse duct just under the disc, and they open as a rule into a capacious bladder which contracts at intervals and expels its contents into the cloaca and thus out of the body. It has been calculated that in some species this bladder expels a bulk of fluid equal to that of the animal about every ten minutes, and this fluid must be replaced by water which diffuses through the body-wall. This water doubtless brings with it oxygen and carries off carbonic acid which it has taken up from the tissues.

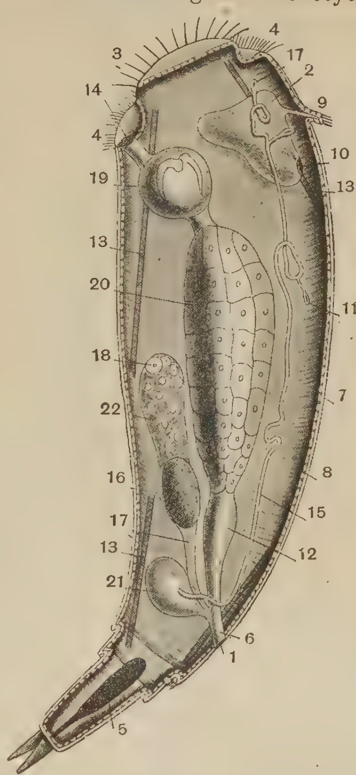


Fig. 52. Diagram of a Rotifer.

1. Anus. 2. Brain. 3. Trochus. 4. Cingulum. 5. Gland in foot. 6. Cloaca. 7. Cuticle. 8. Ectoderm. 9. Dorsal antenna. 10. Eye. 11. A ciliated "tag" of the excretory system. 12. Intestine. 13. Muscles. 14. Mouth. 15. Nephridial tube. 16. Ovum. 17. Oviduct. 18. Ovary. 19. Mastax. 20. Stomach. 21. Bladder. 22. Vitellarium.

The principal part of the nervous system is a bilobed ganglion called the brain. This lies just under the disc on the dorsal side of the mastax; it bears two red eyes in *Floscularia*. In *Notommata* the brain is large, and on it more than one pair of eyes are situated. In the Bdelloida there is also a ganglion on the ventral side of the mastax, and a pair of circumoesophageal cords unite this with the brain. In *Floscularia*, as in Rotifera generally, there are three well-marked sense organs called antennae, consisting of prominences bearing stiff sense hairs;

one is situated in the mid-dorsal line, two are latero-ventral; these latter are in some genera fused with one another.

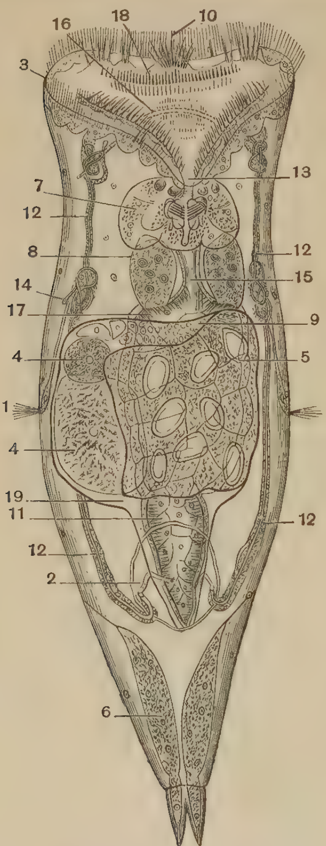


FIG. 53. *Hydatina senta*, ventral view. After Plate. Magnified.

1. Lateral antenna. 2. Bladder. 3. Cingulum. 4. Eggs. 5. Vitellarium or yolk-gland. 6. Foot-gland. 7. Gizzard. 8. Gastric gland. 9. Germarium or ovary. 10. Lobes of "groove" bearing stiff setae. 11. Intestine. 12. Excretory tube. 13. Mouth. 14. Ciliated tag of the excretory system. 15. Oesophagus. 16. Renal commissure or transverse tube uniting kidneys above mouth. 17. Stomach overlaid by reproductive organs. 18. Trochus. 19. Uterus.

As in the Platyhelminthes, so in Rotifers, the ovary, which occupies a good deal of space in the body-cavity, usually consists of a vitellarium or yolk-gland and a germarium or true ovary. The latter lies between the former and the stomach; it is inconspicuous and is more or less hidden by the large cells of the vitellarium. Both glands may be paired. They are enclosed in a membrane continuous with the oviduct, which opens into the cloaca behind the excretory duct.

The above description relates chiefly to the female *Floscularia*, and in fact until 1874 the male was unknown. It is much smaller than the female (B, Fig. 50). As a rule the male Rotifer has a single circlet of cilia, a brain, eyes, excretory system and muscles all more or less reduced, but there is no mouth or alimentary canal. The testis is large and the penis is introduced into the cloaca of the female, or in some cases is thrust through the wall of the body, and then the eggs are probably fertilised in the ovary.

Floscularia lays two kinds of eggs during the summer, both of which are thought to develop parthenogenetically. Both kinds accumulate between the foot and the tube in which the mother lives. The larger eggs, which average five to eight in number,

produce females; the smaller eggs, whose origin seems to be determined by the temperature, may amount to eighteen or twenty. These produce the males. Towards the autumn the males fertilise the females, and the resulting eggs termed "winter-eggs" are clothed with a thick shell capable of withstanding cold and drought. These live through the winter and give rise to females in the spring. A similar alternation of summer and winter eggs is met with in certain Crustacea (Phyllopoda and Ostracoda).

Rotifera are cosmopolitan, but as a rule they inhabit fresh water; about 700 species are known, of which only one-tenth live in the sea or in brackish water. One species, *Synchaeta baltica*, is pelagic and phosphorescent. A few are parasitic. *Hydatina senta* is one of the commonest Rotifers, and is usually to be met with swimming about amongst the algae of green ponds. It possesses a slightly elongated, cylindrical body (Fig. 53). The disc bears a circular cingulum separated by a groove from the trochus; in this groove are five prominences bearing stiff setae. The posterior end of the body tapers and ends in a bifurcated foot on which a pair of glands open.

A great many of the Bdelloida live amongst the roots and leaves of mosses, etc., and these can survive being dried up for a long time, the body shrinking and sealing itself up in the cuticle. Apart from the species which possess this power Rotifera as a class are short-lived, and this is especially true of the males.

In certain respects, such as the nature of their excretory organs and of their ovaries, the Rotifers show some resemblance to the Platyhelminthes; but they differ from them profoundly in the alimentary canal. The velum, in its typical form consisting of trochus and cingulum, has been compared to the ciliated band which encircles the Trochophore larva of Annelida of which more will be related later. This band like the velum is seen on close inspection to consist of a prae-oral and a post-oral loop. The Trochophore larva is found in the life-history of the division of Annelida termed Polychaeta and of some of the more primitive Mollusca, and it is believed by many to represent a common ancestral form. Should the comparison of the Rotifera with this larva be a just one, we must regard the Rotifera as having been derived from the common stock of Annelida and Mollusca and to be therefore a very ancient group. There are however difficulties which arise when the comparison is carried into details, so for the present it is better to regard the Rotifera as a completely isolated phylum.

Leaving out of sight a few parasitic and aberrant forms, the bulk of the Rotifera are classified as follow:

Class I Rhizota.

Rotifera in which the foot is not retractile but forms a permanent organ of attachment. The animal lives in a tube.

Ex. *Floscularia.*

Class II. Bdelloida.

Rotifera which creep like a leech, using the foot as a sucker. They are provided with a protrusible adhesive proboscis on the dorsal surface, by which the anterior end of the animal may be made to adhere.

Ex. *Rotifer.*

Class III. Ploima.

Rotifera which swim freely, only occasionally attaching themselves by the forks of the bifurcated foot.

Ex. *Hydatina, Synchaeta, Notommata.*

Class IV. Scirtopoda.

Rotifera provided with hollow movable outgrowths from the body, by means of which they leap.

Ex. *Pedalion.*

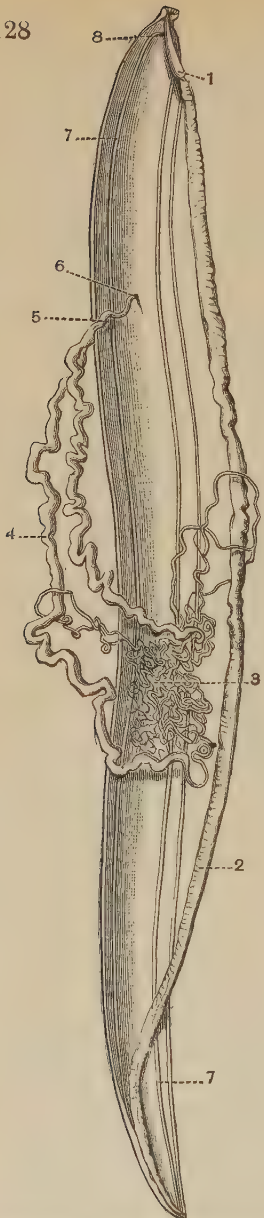
CHAPTER VIII

PHYLUM NEMATODA

The Nematoda include a very great number of species commonly termed Thread-Worms, or from the shape of their cross section Round-Worms. Certain species attain a great length, as long as a man, but more commonly they are small and insignificant and often microscopic. The general shape of the body is cylindrical, usually pointed slightly at each end; the surface is smooth with at most a few bristles, so that they easily insinuate themselves into the cracks in the damp earth, or between the tissues of the animals and plants in which for the most part they live.

As a rule, like most animals which pass their time in the dark, Nematodes are white or whitish-yellow in colour. The body is glistening and smooth, but not slimy. It is ensheathed in a thick cuticle, which is in some cases ringed. No locomotor organs exist, and the animals progress by wriggling, bending first to one side and then to the other. The cuticle, which is moulted about four times during the life of the animal, is secreted by an underlying layer called the ectoderm, in which no trace of cell limits can be detected, but nuclei are scattered in it. Along the middle dorsal and middle ventral lines and along each side, this layer is thickened and projects inward. The median ridges support two nerves, the lateral ridges two canals, which are believed to be excretory.

By these ectodermal thickenings the body-wall is divided into quadrants. In each quadrant there is a layer of longitudinal muscle-fibres of very peculiar appearance. In all muscle-fibres there is a patch of unmodified protoplasm termed sarcoplasm surrounding the nucleus, the rest being modified into those fibrils which are the visible sign of a heightened contractile power. In the Nematoda, in which all metabolism is at a low ebb, only the



outermost layer of the muscle-cell is converted into fibrils, the great bulk consisting of unmodified protoplasm, which is often drawn out into an internal process running towards the dorsal or ventral ectodermal ridge. Muscle-cells of such a character are known only in Nematoda.

The body-wall, which has just been described, encloses a space which is traversed from end to end by the alimentary canal. This space is full of fluid and it lodges the reproductive system. It has no epithelial lining and is a primary body-cavity and the only representative of blood is the fluid which it contains.

The mouth is terminal and is usually surrounded by certain papillae or lobes, often three or six in number. It leads into an oesophagus, usually with a triangular cavity and thick muscular walls (Fig. 54). The oesophagus may be immediately followed by a second muscular bulb, called the pharynx, which sometimes has an armature of some bristles or spines. Both oesophagus and pharynx are parts of the stomodaeum. Then follows the intestine, which is by far the largest part of the alimentary canal. The muscular oesophagus no doubt acts as a sucking organ, but there are no muscles and no cilia in the intestine. It is a simple tube formed of a single layer of cells, which both inside and out secrete a thin cuticle. Posteriorly it passes into a

FIG. 54. Female *Ascaris lumbricoides*, cut open along the median dorsal line to show the internal organs × 1.

1. The muscular oesophagus. 2. The intestine. 3. The ovary. 4. The uterus. 5. The vagina. 6. Its external opening. 7. The excretory canals. 8. Their opening.

proctodaeum with muscular walls, and this terminates in the anus situated a little in front of the end of the tail.

The nervous system consists of a ring round the oesophagus, which sends off in front six nerves to the mouth and its papillae, while behind it also gives off six nerves, the two more important of which run down the body in the above-mentioned median dorsal and ventral ectodermic ridges. Transverse commissures unite these main nerve-trunks at irregular intervals. With the exception of certain hairs and papillae to which a tactile sense has been ascribed, and in the free-living species certain eye-spots, no organs of sense are known in the Nematoda. The excretory function is usually assigned to two long tubes which run along the lateral thickenings of the ectoderm. These tubes end blindly behind, but anteriorly the tubes approach one another ventrally and open by a common pore in the middle ventral line some little distance behind the mouth (Fig. 54). Each of these tubes is stated to consist of one immensely elongated hollow cell. Each is probably to be regarded as a degenerate nephridium.

Nematoda with few exceptions have the sexes separated. The male is often smaller than the female and frequently has a curved tail. In both sexes the reproductive organs are tubular. In the male the organ consists of a long tapering tube much folded on itself opening into the proctodaeum close to the anus. In the uppermost and narrowest part of the tube there is a mass of protoplasm with nuclei; lower down the mother-cells of the male cells become separated, while the lowest part contains ripe male cells. These male cells are not spermatozoa however, but small oval cells with large nuclei capable of only very sluggish amoeboid movement. The names testis and vas deferens are given to the upper part and lower part respectively of this organ, but the whole is one continuous structure developed from a single cell in the embryo. In the female there are two similar tubes which unite to open in the mid-ventral line by an exceedingly short median piece termed the vagina. The vagina is situated about one-third of the body-length from the head. In each tube it is usual to distinguish an upper ovary consisting of a mass of nucleated protoplasm, a middle oviduct where the bodies of the egg-cells have become separated from one another, and lastly a uterus where the eggs after fertilisation are each provided with a shell. Each tube however, like the testis of the male, is developed in the embryo from a single cell.

In order to introduce the motionless male cells the male distends

the vagina of the female by inserting two cuticular hairs, developed from the lining of his proctodaeum, called copulatory spicules.

It is a most peculiar characteristic of the Nematoda, which they share with the great group Arthropoda, that no cilia are found in any organ of their body. Even the male cells have no flagella but move in an amoeboid manner. This absence of cilia, which are found in every other group of the animal kingdom except Arthropods, and which even occur in many plants, has received hitherto no explanation. It is possibly correlated with the strong tendency of the protoplasm in both phyla to produce cuticle. The eggs of Nematoda have a structure well adapted for histological investigation, and have been much utilised in researches on the behaviour of the nucleus before and during fertilisation. As a rule the eggs are laid, but there are many species which produce their young fully formed.

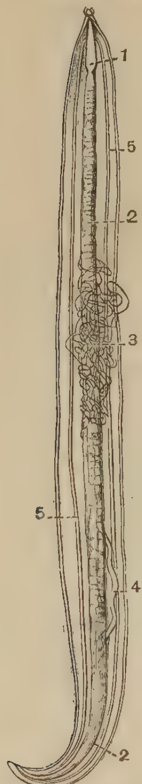


Fig. 55. Male *Ascaris lumbricoides*, cut open along the dorsal middle line × 1. 1. Oesophagus. 2. Intestine. 3. Testis. 4. Vas deferens. 5. Lateral excretory canals.

Comparatively few species are free-living throughout their whole career, but these few are interesting. They are of small size and inhabit damp earth or mud, one family being marine. The mouth is often provided with movable spines and there are frequently eyes. These features suggest a relationship with the Chaetognatha, which, like the Nematoda, have a thick cuticle and only longitudinal muscles; and the idea receives support from the existence of a group of small marine "worms" called the Chaetosomatidae, which are probably also to be regarded as free-living Nematodes. These animals have two semicircles of movable bristles, situated one at each side of the mouth, and in addition a double ventral row of similar spines by means of which they creep about. In this feature and in some others these animals exhibit a resemblance to the Chaetognatha (see pp. 381—384).

Taking the free-living forms as a starting-point we can arrange the other families of Nematoda in an ascending scale of increasing parasitism, culminating in a form like *Trichina spiralis*, which is a

perpetual parasite. This Nematode inhabits the intestine of its host (Pig, Man, etc.) where it lays its eggs. From these eggs larvae hatch out which bore through the walls of the intestine and get into the circulation, by which they are carried all over the body. They encyst themselves in the muscles (Fig. 56) and do not develop further unless the flesh of their host is eaten by another animal, in whose intestine they become mature and then the cycle of development recommences. Their natural host is the Rat; the Pig is a secondary host and being a gross feeder no doubt often devours rats and the remains of its own species, and thus the parasite is propagated. *Trichina* can however live perfectly well in Man, as the prevalence of the disease trichinosis testifies. This disease is contracted by eating insufficiently cooked pork infested by the encysted larvae of *Trichina*. These become mature in the human intestine, and give rise to a second generation which cause severe and occasionally fatal symptoms by boring through the intestinal wall.

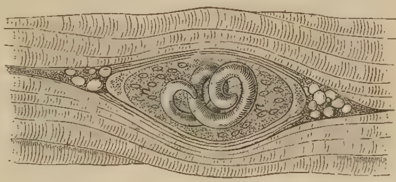


FIG. 56. *Trichina spiralis*, encysted amongst muscular fibres. Highly magnified. After Leuckart.

Most Nematodes pass the earlier part of their existence in damp earth, during which they are known as Rhabditis larvae and bear a strong resemblance to some of the free-living forms. *Tylenchus tritici* forms the so-called Ear-cockles in wheat; these are brown galls replacing the wheat grains and filled with encysted Nematodes. If the grains are beaten to the earth by rain the worms escape from the cysts and climb up the wheat stalks, where, after a generation which live in the flower, they again enter the grains. In *Sphaerularia bombi* the males and females live together in damp earth, but the fertilised female enters the body of a Bee and here develops into a great sac filled with eggs. In *Syngamus trachealis* the eggs are laid in damp earth, and here develop into larvae, which are swallowed by poultry and develop in their windpipes into the sexual form, causing the disease called gapes, which is often fatal. *Filaria sanguinis-hominis* lives in the human lymphatic glands; the embryos escape into the blood, whence they are taken up by the Mosquito in whose body they develop. When the Mosquito bites they make their way again into the blood of Man. They are the cause of a peculiar form of malaria known as "filariasis."

They are believed to be the cause of the strange tropical diseases associated with the name elephantiasis. This disease is due to a clogging of the lymph vessels (see p. 434), the lymph accumulates behind the obstruction, and the cells floating in it give rise to a loose gelatinous connective tissue which causes certain parts of the body to be enormously distended and disfigured. The clogging is due to the fact that under certain circumstances this worm lays *eggs* instead of producing active wriggling larvae. The non-motile eggs choke the smaller crevices of the lymphatic system. But it would lead us too far to enumerate all the modifications of the life-history produced by parasitism. Suffice it to say that the Nematoda are perhaps the most successful of all parasites; there is scarcely a phylum in the animal kingdom which they do not attack. A smooth slippery body which as a general rule causes little inconvenience to the host and a low grade of metabolism requiring small supplies of oxygen seem to have been the leading features in their success.

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CHAPTER IX

INTRODUCTION TO THE COELOMATA

In the groups of Metazoan animals so far studied we have to deal with an external layer of cells called the ectoderm (or in Porifera the dermal layer) which forms the skin, and an internal layer termed the endoderm (or in Porifera the gastral layer), whilst between them is found a space containing a substance which varies from the condition of a semi-solid jelly in Coelenterata to that of a fluid which is almost pure water in Rotifera. In addition except in Coelenterata it contains cells which are developed into processes which stretch across the cavity. And these processes may secrete fibres and become connective tissue or may become developed into muscular fibres. Where the cells and fibres are sparse this space is said to be a primary body-cavity. Where they are abundant it is called parenchyma or connective tissue.

Coelom.

The phyla which are next to be considered, and which may be grouped together under the name Coelomata, differ from those which we have so far considered in the possession of an important organ termed the coelom (Gr. κοίλωμα, a thing hollowed out). This, like the primary body-cavity, is often described as a space intervening between the ectoderm and endoderm, and the terms coelomic cavity and body-cavity have been used to describe it. In spite of the etymological difficulty we propose in the following pages to deal with this organ under the term coelom, and its cavity under the term coelomic cavity. In reality it consists of one or more pairs of sacs with perfectly defined walls lying at the sides of the endodermic tube. In the adult these sacs join each other above and below the endoderm, and the adjacent walls entirely or partly break down, and thus one continuous cavity results. The wall of the coelom and the tissues derived from it are known as the mesoderm. To describe the coelom as a split

or space is to describe it negatively: with as much justice the endodermic tube might be described as a split. In each case the real object of consideration is the wall, and this is the point where the coelom which the Germans appropriately name the secondary body-cavity differs fundamentally from the primary body-cavity, for the outer wall of the latter is merely the ectoderm. In many animals such as Mollusca the two types of body-cavity coexist, and indeed in all the higher animals the vessels or tubes which convey the blood may be said to be remnants of the primary body-cavity.

Fig. 57. Three transverse sections through a developing Amphioxus to show origin of mesoblast from endodermal pouches × 435. From Hatschek.

The ectoderm is deeply shaded, the mesoderm is lightly shaded, the endoderm —alimentary canal and notochord—is unshaded. A. shows the origin of the paired mesodermal pouches from the archenteron; the cavity—coelomic—of the former is still in communication with the cavity of the alimentary canal. The notochord is arising in the middle line from the endoderm, and the tubular nervous system above it is already separated from the ectoderm. B. shows the mesodermal pouches completely shut off; they each enclose a cavity, the coelom, and each consists of an outer wall next the ectoderm, the "somatopleure," and an inner wall next the endoderm, the "splanchnopleure." C. shows the mesodermal pouches extending ventrally beneath the notochord, now completely separated from the wall of the alimentary canal and also round the alimentary canal. The coelomic space is larger, and the splanchnopleur is beginning to form muscle-cells.

If we leave out of account cases in which the facts of development have not been fully elucidated and confine our attention to those instances where the whole history of the coelom has been exhaustively worked out, we find that this important organ arises in one of two ways, either (1) by the formation of pouches of the endodermic tube, which become nipped off (Fig. 57); or (2) by the proliferation of two large cells, formed themselves by budding from the endoderm (Fig. 58), which subsequently grow rapidly and divide so as to form bands, the so-called mesodérmic bands, these bands later become hollowed out. These initial cells are termed pole-cells.

A sharp controversy has raged round the question which of these two processes gives us the best representation of what occurred in the evolution of Coelomata from simpler Coelenterata-like ancestors.

If however we recall the fact that in the Actinozoa the endodermic sac has the form of a series of pouches ranged round a central cavity, and that the walls of these pouches become converted into muscles and generative cells exactly as does the wall of the coelom, and that pores exist in many cases placing the cavity of these pouches in communication with the outside world, we shall

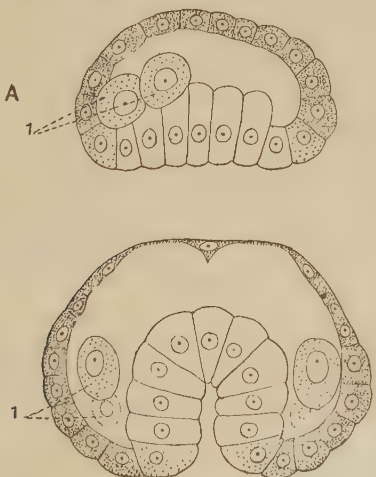

FIG. 58. Two stages in the early development of a common fresh-water mollusc, *Planorbis*, to show the origin of the mesoderm cells × 320. From Rabl.

The ectoderm cells are deeply shaded, the endoderm cells are unshaded. A. Young stage in which the endoderm has not begun to be invaginated; it is a lateral optical section. B. Older stage, optical section seen in front view; the endoderm cells are invaginating, and the two mesoderm cells are seen on each side. 1. Mesoderm or pole-cells; in B, each has budded off another mesoderm cell.

be induced to conclude that the coelom was probably evolved from lateral pouches of the gut and that the mesoderm is therefore derived from the primitive endoderm. Where pole-cells occur the cavity of the alimentary canal is small in proportion to the thickness of its wall, and the pole-cell might be looked on as a solid pouch.

In most Coelomata the mesoderm or coelomic wall forms by far the greatest portion of the body. In the phyla which we have heretofore considered there are usually, as we have already mentioned,

cells in the primary body-cavity. To such cells the name mesoderm has also unfortunately been applied and great ambiguity has resulted from this practice. The term mesenchyme has been proposed for these cells and it is to be hoped that it will be more generally adopted so that the name mesoderm may be confined to the coelomic wall. The origin of mesenchyme is different in different cases. In Actinozoa it appears to arise mainly from the ectoderm, in Ctenophora from the endoderm. In Platyhelminthes it arises principally from the endoderm. In the higher Coelomata it arises partly from the ectoderm but principally from the outer wall of the coelom. Everywhere it gives rise to connective tissue and to the tissues developed from this (tendon, cartilage, bone, etc.), whereas the coelomic wall or true mesoderm gives rise to the generative cells and their ducts, and the main parts of the muscular system including the muscular coats of the principal blood-vessels.

The endoderm, after the separation from it of the mesoderm, forms the lining epithelium of the digestive tube and of its appendages, which in the higher Vertebrata are the organs known as lungs, liver, pancreas, and urinary bladder. The basis of the skeleton of Vertebrata, the gelatinous rod called the notochord, also arises from it.

We have already seen that the ectoderm can be intucked both at mouth and anus so that both in front and behind there is an ectodermal section of the alimentary canal. The anterior of these sections we have already learnt is called the stomodaeum and the posterior the proctodaeum. In Crustacea these sections form by far the greatest sections of the alimentary tube.

The internal anatomy of the lower animals was first studied by physicians and others who were primarily interested in human anatomy. An unfortunate consequence is that a large number of names are used in the description of simpler animals which are based on fanciful resemblances between their organs and those of man. As a consequence many of these names are quite misleading. To give some instances: the word stomach in the Lobster denotes part of the stomodaeum, in the Vertebrata it signifies part of the endodermic tube. The pharynx of an earthworm is the stomodaeum, in a fish it includes both stomodaeum and the first part of the endodermic tube. The term liver has also been much abused.

The names taken from the anatomy of the higher animals which are customarily used in the description of the alimentary canal are as follows: mouth- or buccal-cavity, pharynx,

oesophagus, stomach or crop, gizzard, intestine, and rectum. They are applied generally to parts of it succeeding one another in the order above given. The significance of these will be explained in each case: it would perhaps be more logical to sweep away altogether these and a host of similar terms employed to designate other parts of the body, but so deeply are they engrained in zoological literature that such a course would render unintelligible most anatomical descriptions of species that we possess.

Besides forming the outer layer of the skin or epidermis of the animal and the stomodaeum and proctodaeum, the ectoderm gives rise to the brain and nervous system and to the essential cells of the sensory organs.

CHAPTER X

PHYLUM ANNELIDA

The name Annelida (Lat. *annulus*, a ring) means ringed, and refers to the fact that the bodies of the creatures grouped under this name are built up of a series of parts more or less resembling each other placed one behind another. This division of the body into more or less similar parts is called segmentation; each part is called a segment (or somite), and the animal is said to be segmented. Like the symmetry, the segmentation may be merely external or may affect both the exterior and a greater or less number of the internal organs. Sometimes, however, as in the case of the longer half of an earthworm's body, the segmentation affects all the organs, and the likeness of one segment to another is so great that it would be impossible to say what part of the body any given isolated segment was taken from. More often, however, one or another of the organs of the body differs in shape or size in successive segments, and this is the case with the internal organs of the first twenty segments of the earthworm's body, so that if these segments were all separated it would not be very difficult to place them together in their natural order.

Segmentation.

The Earthworm. External features.

If we take an earthworm and kill it by placing it in alcohol for a few minutes and examine it carefully, we shall see that the body is composed of some 150 rings, each of which corresponds with a segment. The rings are separated from one another by slight grooves. At each end of the body there is an opening, the mouth (2, Fig. 59) in front and the anus (3, Fig. 59) behind. Besides these, two slit-like pores with rather swollen lips, situated on the under surface of the fifteenth segment (5, Fig. 59), may be seen. These are the pores through which spermatozoa are discharged, and

are consequently known as the male genital openings. The other openings into the body are minute and require the aid of a lens to make them out. There are paired openings on each segment, except the first three and the last, situated latero-ventrally; these are the openings of the nephridia; in addition to these a median dorsal pore opening into the body-cavity is situated in each groove behind the tenth segment (11, Fig. 63). The earthworm is hermaphrodite, that is, it contains both male and female organs in its body. Through two slit-like openings in the ventral surface of the fourteenth segment the eggs are discharged: these are called the female generative openings. Two pairs of pouches called spermathecae, which are reservoirs for spermatozoa received from another worm (*v.* p. 97), open, one pair between the ninth and tenth, the other between the tenth and eleventh segments, all on the ventral surface.

If a worm killed in alcohol be drawn through the fingers a certain roughness may be felt along the sides and lower surface. This roughness is due to the presence of a number of small bristles, called chaetae (Gr. χαίτη, hair), which project from the body (7, Fig. 59, and Fig. 62). Each segment bears eight of these chaetae arranged in four pairs, one pair on each side being lateral and the other nearer the ventral middle line. It is by means of the chaetae that the worm crawls about; since by protruding the chaetae and implanting them in the soil a fixed point is obtained from which the anterior end of the

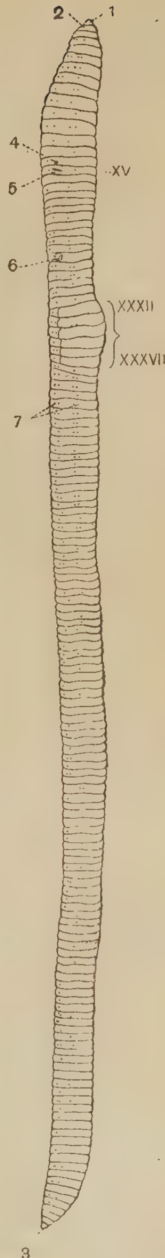

FIG. 59.

FIG. 59. Latero-ventral view of *Lumbricus terrestris*, slightly smaller than life-size. From Hatschek and Cori.

1. Prostomium. 2. Mouth. 3. Anus. 4. Opening of oviduct. 5. Opening of vas deferens. 6. Genital chaetae. 7. Lateral and ventral pairs of chaetae.

XV, XXXII, and XXXVII are the 15th, 32nd, and 37th segments. The 32nd to the 37th form the clitellum.

body can be pushed forward and to which the hinder end of the body can be drawn up.

The colour and thickness of the body from the thirty-second to the thirty-seventh segment differ in adult worms from those of the segments which lie before and behind this band. This is due to the presence in this region of certain ectodermal glands whose secretion forms the cocoons in which the eggs are laid. This region of the body is called the clitellum (XXXII—XXXVII, Fig. 59).

The surface of the body of an earthworm is glistening and somewhat slippery. This is due to the cuticle, which is a thin membrane secreted by the ectoderm cells of the skin; if a dead earthworm be soaked in water for a few hours the cuticle can be easily stripped off the body. As we have already seen a similar cuticle is present in Trematoda, Cestoda, Nematoda and Rotifera, but in the two groups last mentioned it is much harder and forms an external protective skeleton; even in the earthworm, where it is soft, it acts as a protection to the underlying cells, and its smooth surface enables the worm to creep into narrow holes without hindrance. The chaetae are simply large local thickenings of the cuticle: they protrude from pockets called chaeta-sacs, each of which is a portion of the ectoderm tucked in. In the bottom of each sac is a specially large cell which rapidly secretes a column of cuticle and builds up the chaeta.

Internal Anatomy.

If we cut through the skin of an earthworm we do not make our way into the cavity of the alimentary canal but into the coelomic cavity, in which not only the alimentary canal but the blood-vessels, kidneys and reproductive organs apparently lie. The relation of the coelom in the earthworm to the ectoderm and endoderm may be illustrated in the following way. Take a piece of leaden gas-tube or of thick glass tubing to represent the endodermic tube or alimentary canal, slide over it a series of hollow rubber rings so that these rings are pressed closely against one another in longitudinal series. Then pull a cotton casing over the whole thing and so we shall have a rough model of the body of an earthworm. The cotton casing will represent the ectoderm and the rubber rings collectively the coelom. From this we learn that the coelom of the earthworm consists not of one but of a series of cavities—there being one ring-shaped cavity in each somite, and that these cavities are separated from one another by transverse walls which are called septa or dissepiments. Each cavity has its own proper wall which is termed

peritoneum (Gr. περί, around; τόνος, a string). Where this wall adjoins the ectoderm it is called parietal or somatic peritoneum (Lat. *paries*, an outer wall; Gr. σῶμα, body), where it impinges on the gut it is called visceral or splanchnic peritoneum (Lat. *viscus*; Gr. σπλάγχνον, entrail). A septum consists of two layers of peritoneum—one forming the hinder wall of the coelomic space in front and the other the front wall of the coelomic space behind, and intervening between the two there is a certain amount of mesenchyme in the form of connective tissue and also channels for the blood. Each septum is pierced with a small hole in the mid-ventral line so that fluid can pass from one coelomic cavity to the next.

Like all similar spaces in animals the body-cavity of an earthworm contains a fluid, and in this fluid certain cells float which change their shape as an *Amoeba* does, and hence are called amoebocytes. As a rule the coelom is completely shut off from the outside world, but in the earthworm it opens to the exterior by means of the dorsal pores (11, Fig. 63), and at times the fluid which it contains escapes through these holes and pours over the cuticle. This fluid has a certain poisonous action on bacteria, and helps to keep the outside of the body clean and free from parasites. Somewhat similar pores leading from the exterior to the body-cavity are found in certain fishes.

The first segment is divided into two parts, viz. (*a*) a lip or prostomium (1, Fig. 62), overhanging the somewhat crescent-shaped mouth, and (*b*) a peristomium containing the mouth which leads into an oral cavity extending through three segments (Fig. 60). There are no teeth in this cavity and the food is probably sucked in by the action of the muscular stomodaeum, called the pharynx, which succeeds it and reaches back to the sixth or seventh segment. This is followed by the true endodermic tube. The first part is narrow and is called the oesophagus; it reaches to the twelfth segment and has three pairs of lateral pouches developed on its walls. These pouches secrete calcareous particles, and hence are termed calciferous glands. Their formation has recently been carefully investigated by Stephenson and it is interesting. The most anterior pair open widely into the oesophagus of which they are merely lateral dilatations: folds project into their cavities. As we pass back the free edges of these folds unite so that the spaces between them form a series of tunnels and these tunnels make up the middle and posterior pair of glands. The oesophagus dilates behind into a thin-walled sac, called the crop, situated in the region

of segments thirteen to sixteen, and this is separated by a groove from a thick-walled sac, with hard, horny walls, termed the **gizzard**, which extends to about the twentieth segment. The exact segment in which the above-mentioned parts of the alimentary canal lie varies with the amount of food they contain, the septa which are pierced by them being stretched forward or backward according to their state of fulness or emptiness.

Behind the twentieth segment the intestine stretches without change to the anus. It is a thin-walled tube, supported by the septa between each segment and swelling out slightly in each segment, so that it presents an outline like a string of beads. A deep fold, called the **typhlosole** (Gr. τυφλός, blind; σωλήν, a gutter), runs along the upper surface of the intestine, projecting into its cavity. Its presence causes the wall of the intestine to be pushed in, and thus its internal absorbing surface is increased (7, Fig. 61). The intestine is covered everywhere by a number of cells of a **yellow colour**. These form the inner wall of the coelomic sac and are actively engaged in excretion.

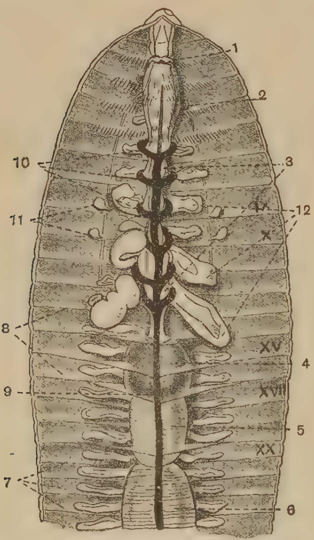

FIG. 60. Anterior view of the internal organs of an Earthworm, *Lumbricus terrestris*. Slightly magnified. From Hatschek and Cori.

1. Central ganglion or brain. 2. Muscular pharynx. 3. Oesophagus. 4. Crop. 5. Muscular gizzard. 6. Intestine. 7. Nephridia (the reference lines do not quite reach the nephridia). 8. Septa. 9. Dorsal blood-vessel. 10. Hearts. 11. Spermathecae. 12. Vesiculae seminales.

The Roman figures refer to the number of the segments.

The exact part that each of the above-mentioned parts of the alimentary canal plays in digestion is not thoroughly understood. The pharynx helps to take food in by a sucking action which is caused by the contraction of the muscles running from it to the body-wall, resulting in an enlargement of the cavity of the pharynx so that food may pass in by atmospheric pressure. The food passes down the oesophagus, being propelled by a series of contractions of the walls of the

alimentary canal which push it along; on its passage it is mixed with the secretions of the calciferous glands. It has been suggested that since the decaying vegetation on which the worm feeds is strongly acid in character the calcareous particles secreted by the calciferous glands tend to neutralise these acids. The crop serves as a resting-place in which the food accumulates before passing into the gizzard. The hard, horny walls of the last-named chamber help to grind up the food and render it fit for the action of the juices which digest it. The process of digestion, or the rendering of the food soluble, probably takes place in the intestine, and through the walls of this portion of the alimentary canal the soluble products of

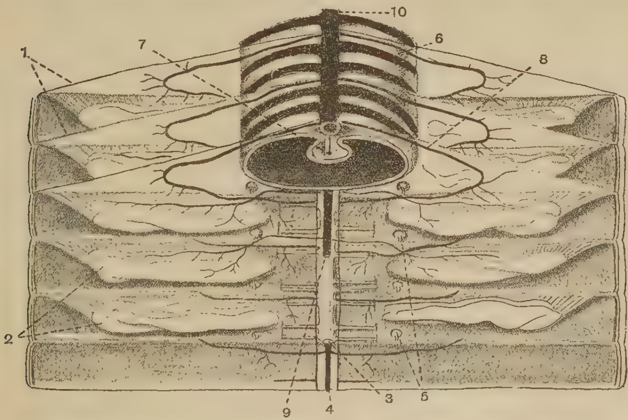

Fig. 61. Six segments from the intestinal region of an Earthworm, *Lumbricus terrestris*, dissected to show arrangement of parts. Magnified. From Hatschek and Cori.

1. Septa. 2. Nephridia. 3. Ventral nerve-cord. 4. Sub-neural blood-vessel. 5. Nephrostomes, internal funnel-shaped openings of nephridia. 6. Intestine. 7. Typhlosole. 8. Circular blood-vessels. 9. Ventral or sub-intestinal blood-vessel. 10. Dorsal blood-vessel.

digestion soak, and are taken all over the body by the blood-vessels and probably also to some extent by the fluid in the coelom.

The series of contractions which squeeze the food onwards towards the anus are known as peristalsis; they constitute the sole movements of which the alimentary canal is capable and are carried out by muscles developed from the cells of the inner wall of the coelom, which pass round the canal like a series of rings or tight india-rubber bands.

The earthworm eats earth and manages to find sufficient nourishment for its needs in the small amount of organic matter,

broken-down débris of leaves, etc., which is contained in the earth. The actual minerals of the earth are not digested but are passed out of the body in the form of those coiled and thread-like castings which are so commonly seen on a lawn in the early morning. Earthworms also eat fallen leaves and to this end they drag the leaf-stalks into their burrows, and on autumn mornings it is a common sight to see lawns studded with the stalks of horse-chestnut leaves or the needles of fir trees, the stalks having been dragged a little way into the burrows by the worms. The burrows that they make admit both air and rain to the deeper layers of the soil, and the earth which they swallow in their burrows is brought to the surface and spread about in the form of castings. This is carried on to such an extent that the whole surface of the soil soon becomes covered by a layer of earth brought up from below. It is thus clear that the earthworm is of great use as an agricultural agent.

All the blood-vessels are remnants of the primary body-cavity which is nearly obliterated as the result of the expansion of the secondary body-cavity or coelom—they may be described as being merely crevices between the coelomic wall on the one hand and the ectoderm and endoderm on the other. Those mentioned below are merely the larger channels in a continuous network of spaces. The contractile power which some, like the hearts, dorsal vessel, and sub-intestinal vessel, possess is due to the presence of a special wall of muscular cells derived from that part of the coelomic wall which lies next them. A few of the blood-vessels seem also to have an inner wall consisting of flattened cells—this is known as an endothelium. Its origin is curious and interesting. In the blood of the earthworm as in that of almost all animals there are floating cells which, like those in the coelom, resemble *Amoeba* in the power of crawling and of emitting pseudopodia; certain of these amoebocytes adhere to the walls of the crevice which constitutes the blood-vessel, become flattened and make in this way an almost complete plating of cells.

The fluid in the primary body-cavity is the medium into which the digested product of the food diffuses from the endoderm cells, and in which the excreta accumulate until they are removed by the excretory organ. The oxygen necessary for the respiration of the mesenchyme cells must also diffuse into it through ectoderm or endoderm or both. Hence this fluid which is the basis of blood has three main functions: (*a*) it conveys the products of digestion to

the internal cells of the body, (*b*) it conveys excreta to the excretory organ, and (*c*) it conveys to the internal cells of the body the oxygen necessary for their respiration.

The most important blood-vessels of the earthworm are as follows: (1) a dorsal blood-vessel visible through the skin as a dark streak which runs along the body of the worm from head to tail in the middle line (10, Fig. 61); (2) a parallel sub-intestinal vessel which underlies the intestine, and (3) a third but smaller vessel, the sub-neural, which lies still more ventrally under the nerve-cord. There are also two latero-neural vessels lying one at each side of the sub-neural vessel, but as they are connected with it at frequent intervals the three together may be regarded as practically one vessel. The dorsal vessel receives blood from the yellow cells covering the intestine by two pairs of minute vessels in each segment, and anteriorly it breaks up into a network of small vessels which branch over the pharynx. Two vessels in each segment connect the ventral vessel with the network of fine blood-vessels which covers the surface of the alimentary canal, and the ventral vessel and the dorsal vessel are connected by means of five pairs of loops, called hearts, situated in the seventh, eighth, ninth, tenth, and eleventh segments (10, Fig. 60). The dorsal vessel and the sub-neural vessel are put into communication in each segment by two parietal vessels which lie on the outer wall of the coelom and which receive numerous small vessels from its substance. Each nephridium is connected by one vessel with the ventral vessel and by another with the parietal vessel.

The earthworm breathes through its skin. The parietal vessel sends up into the skin innumerable minute vessels or capillaries which come so near the outer surface of the worm that the oxygen can pass in from the air into the blood. The name capillary (Lat. *capillus*, a hair) was suggested by a comparison of the exceedingly small calibre of these vessels with the diameter of a human hair.

The blood is red, and the red colour is due to the same substance which colours our blood, haemoglobin, but there is this difference, that whereas in Vertebrates the haemoglobin is contained in certain cells which float in an almost colourless fluid, in the earthworm it is dissolved in the fluid itself. This substance has a strong attraction for oxygen, which it takes up from the air that comes into the neighbourhood of the skin-capillaries, forming a bright red compound called oxy-haemoglobin. This compound is unstable, and when the blood in its course round the body encounters a cell

hungry for oxygen, the oxy-haemoglobin is decomposed: the reduced haemoglobin is purplish in colour. At the same time the cell gives up carbon dioxide to the blood. The relations of this gas in the blood are less understood than those of the oxygen, but like the latter it is in loose chemical union, though not with the haemoglobin. In Vertebrate animals the sodium of the blood provides the means of conveying the carbon dioxide to the respiratory organs. When the blood again approaches the skin carbon dioxide is got rid of, oxy-haemoglobin being again formed by fresh oxygen taken in.

The earthworm is the first animal which we have so far studied in which there is any flow of the blood in a definite direction—in a word a circulation. Movements of the fluid contained in the vessels of the Nemertine worms in various directions are doubtless occasioned by the contractions of the body muscles of those long thin animals—in the Rotifera owing to their small size the whole bulk of the fluid is so small that the molecular movements of diffusion are enough to thoroughly mix it up. The direction of movement of the blood in the dorsal vessel in the Earthworm can be seen through the skin. Waves of contraction are seen to begin in the hinder end of this vessel and to travel forwards, pushing the blood in front of them. In the other vessels the direction of the flow can be inferred from the existence of valves. These are flaps projecting inwards from the walls of the vessels into their cavities. They are arranged in pairs so as to open only in one direction. When they swing in the opposite direction they come together and close the cavity of the vessel. The blood must therefore flow in the direction in which the valves open. In the dorsal vessel there is in each segment a pair of valves opening forwards. Where the parietal vessel joins the dorsal vessel there is a pair of valves opening upwards, and lastly in each heart there is at each of three different levels a pair of valves opening downwards. Hence we infer that as blood flows forwards in the dorsal vessel, blood pours into it from the parietal vessel which has ascended from the sub-neural vessel along the outer side of the body. Some of this blood has doubtless passed into the dermal plexus, as the network of fine vessels is termed which underlie the skin and are connected with the parietal vessel. In this plexus the blood has been recharged with oxygen. Blood passes from the dorsal vessel downwards into the ventral vessel through the hearts, and as this latter vessel is devoid of muscles and valves it is to be regarded as a reservoir in which the blood is stored and from which it passes out in all

directions. Thus some of it descends to the sub-neural vessel by a vessel situated in each septum. Some of it streams out to the gut and enters the plexus of fine vessels surrounding it in which it absorbs the products of digestion and passes by other vessels into the dorsal vessel; and some of it streams out to the nephridia, is there relieved of its nitrogenous excreta, after which it passes on to the parietal vessel. Blood from neural vessels and nephridia passes upwards in the parietal vessel to pour into the dorsal vessel.

In the earthworm the excretion of the waste nitrogenous material is carried out by the nephridia. They are distributed throughout the body, one pair being situated in each segment, except the last segment and the first three, which have no nephridia (7, Fig. 60, and 2, Fig. 61). The nephridia differ from those of Platyhelminthes, Nemertinea and Rotifera, (1) in being unbranched, since each consists of a single coiled tube, and (2) in that each opens into the coelom at its inner end by a funnel termed the nephrostome. This nephrostome has cilia on its funnel-shaped rim, and these flicker with an untiring movement. The nephrostome does not lie in the same segment as the rest of the tube but pierces the anterior septum, and projects into the cavity of the segment in front, somewhere near the sub-intestinal vessel. Thus each segment contains a funnel-shaped opening and a tube which opens externally, but they do not belong to the same nephridium. The tube is not straight but is coiled and lies as a white glistening tangle close to the septum in front. Close inspection shows it to be completely enveloped in a loose fold of the peritoneum forming the hinder wall of the septum.

When we examine a nephridium through a microscope we see that the walls of the tube are very richly supplied with minute blood-vessels. The tube is really a cord of glandular cells placed end to end and traversed by a minute cavity. It is these cells which take up the waste nitrogenous matter from the blood and convey it out of the body. The part of the nephridium nearest the external opening is swollen so as to form a bladder. The cavity is here intercellular instead of piercing the cells themselves, and surrounding it is a muscular wall by the contraction of which the contents are from time to time expelled.

The blood thus takes digested food to the living cells all over the body and brings from them certain nitrogenous excreta to the nephridia, which cast them out of the body. But the nephridia also exert some action on the other great fluid of the body—the coelomic fluid—which bathes all the organs of the body. It has

been mentioned above that the funnel-shaped ciliated openings of the nephridia open into the coelom, so that the fluid of this cavity can pass out of the body not only by the dorsal pores but by the tubular nephridia. This fluid has suspended in it numerous amoebocytes (*v.* p. 141), and these corpuscles act as scavengers, taking up into themselves any foreign bodies, such as bacteria, which have made their way into the coelom, and breaking them up.

The yellow cells (7, Fig. 63), which surround the gut and form the inner wall of the coelom, are also actively engaged in extracting nitrogenous waste from the endoderm cells and the blood-vessels which pass near them. When the excreta have accumulated to a certain extent in a yellow cell it dies, and its remains fall out into the coelomic fluid, where they are eaten by the amoebocytes. These latter then escape by the dorsal pores since the funnel of the nephridium is too small to admit the amoebocytes—it serves merely as a flushing apparatus, since its cilia draw in water from the coelom which is swept down the tube and carries the excreta into the terminal bladder whence they are from time to time expelled.

In the yellow cells we see evidence that the coelomic wall takes part in the process of removing excreta from the blood, and as we ascend in the scale of animal life we shall find that the primitive ectodermic nephridia are more and more replaced by structures derived from the coelomic wall.

The earthworm, although it lives in earth, has a clean, glistening look, and this is partly due to the fact that the coelomic fluid is poured out from the dorsal pores (11, Fig. 63) and keeps the skin moist and lubricated. This fluid is also antiseptic in its action, and thus its presence prevents foreign organisms, such as bacteria, which swarm in the mould in which the worm lives, from settling upon the skin and growing there. Numerous glandular cells belonging to the ectoderm also pour forth a secretion through minute pores in the cuticle.

The Nervous System.

If we cut open an earthworm by a median dorsal incision and attentively examine the upper surface of the pharynx we shall find at its anterior end, tucked away between it and the skin, two little whitish knobs lying close to one another. These are the cerebral or supra-pharyngeal ganglia (1, Fig. 60; 2, Fig. 62). At their outer ends the supra-pharyngeal ganglia pass into two cords (3, Fig. 62). If we now cut away the pharynx and remove the alimentary canal we can trace these two cords towards the ventral middle line where they unite and form the first ventral ganglion (4, Fig. 62): from this a long white cord—the ventral nerve-cord—runs back to

the extreme posterior end of the animal. If we examine these structures with a lens we shall be able to see that the supra-pharyngeal ganglion gives off small nerves to the sensitive prostomium, and that the ventral nerve-cord swells out between each pair of septa, that is, in each segment, into a thicker portion or ganglion which gives off both dorsally and ventrally and on each side three pairs of nerves to the surrounding parts.

The nervous system of an earthworm thus consists of two supra-pharyngeal ganglia situated in the third segment, a pair

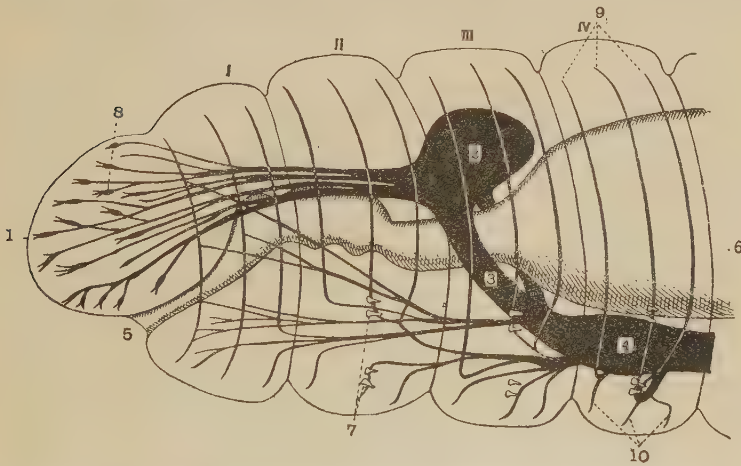

FIG. 62. Diagram of the anterior end of *Lumbricus herculeus* to show the arrangement of the nervous system. After Hesse.

I, II, III, IV. The first, second, third, and fourth segments.

1. The prostomium. 2. The cerebral ganglia. 3. The circumoral commissure. 4. The first ventral ganglion. 5. The mouth. 6. The pharynx. 7. The dorsal and ventral pair of chaetae. 8. The tactile nerves to the prostomium. 9. The anterior, middle and posterior dorsal nerves. 10. The anterior, middle and posterior ventral nerves.

of connecting cords called commissures which form a ring round the pharynx, and a ventral cord which swells out into a ganglion in every segment behind the third. The ring round the mouth and the solid nature of the nervous system are features common to nearly all the Invertebrata, and in those which have a bilateral symmetry and are segmented there are supra-pharyngeal ganglia and a ventral nerve-cord bearing segmentally repeated ganglia.

The nervous system is one of the most important organs of the body. It governs and controls the action of every tissue and cell. It receives and registers impressions from the outside world and co-ordinates the movements and activities of every part of the body.

It further serves to put each organ and each part of each organ in communication with all the others, and thus this vast accumulation of tissues and cells acts in an orderly way and towards a set end. It is built up by the repetition of a special type of cell called the *neuron* or *nerve-cell*. This cell consists of a body containing the nucleus and processes. From the body is given off a straight fine process called the *axon*, which ends in a tuft of processes called *terminal dendrites*. From the other end of the cell a coarse process proceeds outwards, ending in a tuft of processes called *receptive dendrites*. These receive impressions which are transmitted to the axon and passed on either to other neurons or to muscles.

The swelling called a ganglion is due to an aggregation of a number of the bodies of neurons, so that in this region the nerve-cord is broader than at other places, though everywhere some bodies can be seen in transverse section of the cord.

The earthworm has no specialised sense organs, it has neither eyes to see, nor nose to smell, nor ears to hear with. Still, although it is apparently deaf, it is not devoid of the power of appreciating those stimuli which in us excite the sensation of sight or smell. A strong light suddenly turned on the anterior end of the body will cause the worm instantaneously to withdraw into its burrow, and worms readily recognise the presence of such favourite food as onions and raw meat. Their sense of touch is well developed and they are very sensitive to vibrations; for instance, a stamp of the foot on the ground will cause all those in a certain radius to disappear into their burrows. It is further possible that earthworms possess other senses with which we are totally unacquainted.

In each segment of the worm scattered here and there amongst the ectoderm cells are a number of sense cells. Each of these has a minute sense hair which projects upwards through a hole in the cuticle, and by means of this hair stimuli of various kinds are received from the outer world. The body of the cell is small—just large enough to contain the nucleus—and from the base proceeds an *axon* which runs inwards and terminates inside the central nerve-cord in a brush of terminal dendrites in close contact with the receptive dendrites of a neuron. In this way the neurons receive impressions from the outside world. A bundle of the axons of sense cells proceeding inwards is known as a *sensory peripheral nerve*. The receptive dendrites of the neurons receive the impressions from the sensory nerves and pass them on

to other neurons and eventually to muscles. A bundle of axons passing out to a muscle is called a motor peripheral nerve.

A transverse section of an earthworm, such as can be cut by a microtome from a specimen embedded in paraffin wax, is most instructive, in exhibiting the relation to one another of the various tissues which make up the body of the earthworm. The outermost

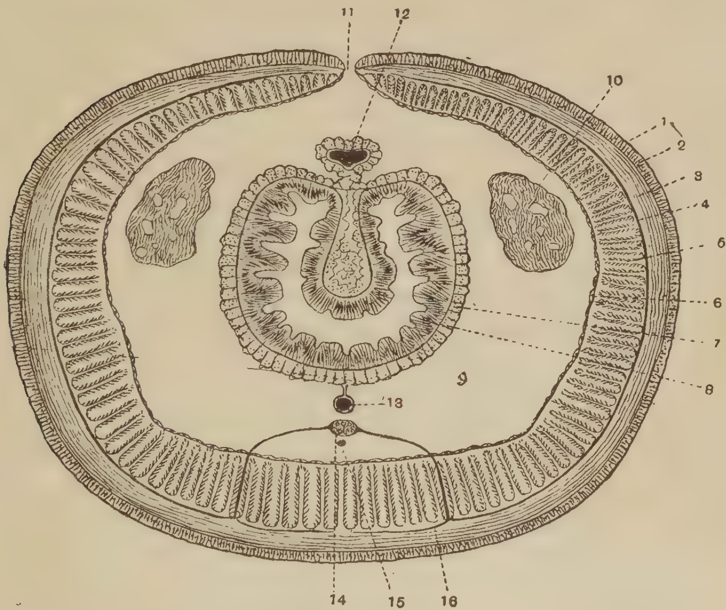

FIG. 63. Transverse section through *Lumbricus terrestris* in the region of the intestine and of a dorsal pore. Magnified.

1. Cuticle. 2. Ectoderm or epidermis. 3. Circular muscles. 4. Dorsal nerve. 5. Longitudinal muscles. 6. Parietal peritoneum. 7. Visceral peritoneum or yellow cells. 8. Endoderm or epithelium lining the intestine. 9. Coelom. 10. Nephridium cut in section. 11. Dorsal pore. 12. Dorsal blood-vessel lying along the typhlosole or groove in the wall of intestine. 13. Sub-intestinal blood-vessel. 14. Ventral nerve-cord. 15. Sub-neural blood-vessel. 16. Ventral nerve.

The dorsal and ventral nerves are added diagrammatically. The other structures are drawn from nature.

boundary is constituted by the cuticle (1, Fig. 63), a hardened secretion poured out by the ectoderm (2, Fig. 63). The ectoderm is composed of tall cylindrical cells, amongst which are isolated "goblet cells"—that is, cells with a round body situated beneath the level of the rest and with a long neck. The name is suggested by their shape. In the body of these cells mucus is

secreted, which is poured forth through a hole in the cuticle opposite the end of the cell-neck and helps to keep the surface of the worm moist.

Beneath the ectoderm is a thin and hardly perceptible layer of connective tissue forming a bed on which the ectoderm cells rest. This foundation is called the dermis, and is included with the ectoderm in the ordinary conception of the "skin." In contradistinction to the dermis the ectoderm is often spoken of as the epidermis (Gr. ἐπί, upon).

Beneath the dermis comes a layer of circular muscles (3, Fig. 63), and beneath these again a much thicker layer of longitudinal muscles. The circular muscles consist of a few layers arranged to form rings round the section. The longitudinal muscles are arranged very regularly, and in the section they have the form of a series of feathers (5, Fig. 63), since the individual fibres appear arranged in oblique rows between which tongues of connective tissue extend, giving off lateral branches on which the fibres rest.

Both sets of muscles are composed of muscle-cells. These are long fibre-like structures pointed at both ends. Most of the protoplasm is differentiated into fine fibrillae, which indicate (see p. 33) contractile power. In the centre of the cell is a patch of unmodified protoplasm with a nucleus. The whole cell may be compared to a myo-epithelial cell of *Hydra* in which the epithelial part has diminished in size and the tail increased. Nor is this a fanciful comparison, for the study of development teaches us that the cell is actually derived in this way from the originally simple cells of the wall of the coelomic sac or in the case of the circular muscles from an ectoderm cell.

The movements of the earthworm can be more easily understood when the arrangement of the muscles is known. The longitudinal muscles serve to shorten the body, and as the coelomic fluid, like water, is practically incompressible, the diameter of the animal must be increased, and thus the chaetae can be driven into the sides of the burrow. On the other hand, the circular muscles diminish the diameter of the coelom, and the contained fluid being forced to move in a longitudinal direction stretches the body out. The holes in the septa equalise the pressure in the various segments by permitting the fluid to escape from one into the next.

Within the longitudinal muscles there is a layer of cells called the parietal peritoneum (6, Fig. 63) which forms the immediate wall of the coelom. The parietal peritoneum is composed of flattened cells; the visceral peritoneum which forms the inner

wall of the coelom, on the other hand, consists of large cubical cells, the yellow cells already described.

Beneath the visceral peritoneum there is a thin layer of circular muscles, the visceral muscles derived from the peritoneal layer and forming the agency by which the peristalsis (*v.* p. 143) of the gut is carried out.

The endoderm (8, Fig. 63) consists of a single layer of long cylindrical cells bent in dorsally to form the typhlosole. Within the limbs of this fold the splanchnic peritoneum is very much thickened.

The dorsal blood-vessel can be seen embedded in the yellow cells lying in the typhlosole (12, Fig. 63), whereas the ventral vessel is attached by a membrane to the ventral side of the intestine. This membrane is really a part of the partition which separated the two coelomic sacs which originally existed in the segment.

The nerve-cord, apparently lying loosely in the coelom, is surrounded by a layer of cells similar to those forming the parietal peritoneum of which they once formed a part (14, Fig. 63). Hence the coelom has extended in a ring-shaped manner round the nerve-cord exactly as it has surrounded the gut. At the sides of and below the nerve-cord may be seen sections of vessels, the sub-neural and latero-neural vessels. The mass of the nerve-cord is made up of the sections of axons, whilst the nuclei of neurons can be seen forming a sheath on the outer border of the cord. The fibres are divided into two bundles by a septum of connective tissue. On the dorsal surface of the cord there are seen three apparent tubes, which are sections of the so-called "giant" fibres—colossal axons which are outgrowths of correspondingly large neurons.

Chaeta-sacs and nephridia cut across may be seen in some sections of the worm.

Reproductive Organs.

It has been mentioned above that it is one of the characteristics of the coelom that the cells lining it should produce the reproductive cells. This does not mean that any cell lining the coelom can become an ovum or a spermatozöon, but that at certain spots the cells forming part of the coelomic wall turn into either female or male generative cells. In the earthworm the paired ovaries (5, Fig. 64) are situated in the thirteenth segment and may be seen by cutting through the intestine about the region of the gizzard and gradually lifting it up from behind forwards; when it is freed up to the twelfth segment the ovaries may be seen as minute white pear-shaped bodies lying one on each side of the nerve-cord. They are attached by their broad end to the posterior wall of the septum separating segment

twelve from segment thirteen, and they are formed by the accumulation and growth of some of the cells which cover this septum, that is, from cells lining this portion of the coelom.

If one of the ovaries be removed and examined under a microscope it will be seen that many of the cells composing it are large, spherical and crowded with granules. The largest lie in the narrow end of the ovary which waves about in the coelomic fluid. These cells are the full-grown eggs or ova and when ripe they drop off from the ovary into the coelom, but are probably at once taken up by the wide funnel-shaped openings of the oviducts, one of which is situated opposite each ovary. Like the nephridia, the two

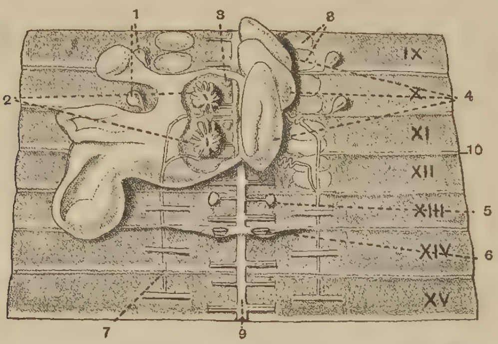

FIG. 64. View of reproductive organs of the Earthworm, *Lumbricus terrestris*. Part of the vesicula seminalis is cut away on the left side to expose the testis and the inner opening of the vas deferens. Slightly magnified. From Hatschek and Cori.

1. Spermathecae. 2. Funnel-shaped internal openings of the vas deferens. 3. Anterior testis. 4. Vesiculae seminales. 5. Ovary attached to posterior wall of septum separating XII and XIII. 6. Oviduct traversing septum separating XIII and XIV. 7. Vas deferens. 8. Glands in the skin. 9. Ventral nerve-cord. 10. Septum.

The Roman figures indicate the number of the segments.

oviducts pierce a septum, the one between the thirteenth and the fourteenth segments. They are short tubes which open into the coelom by the above-mentioned funnel-shaped opening in the thirteenth segment and to the exterior by a small pore just outside the inner pair of setae on the fourteenth (6, Fig. 64). They bear on their course a diverticulum or sac which is called the receptaculum ovorum, in which the ova collect until the earthworm is ready to make a cocoon to receive them.

The male reproductive cells are formed in the testes, of which there are two pairs situated in a similar position to the ovaries but in the tenth and eleventh segments (3, Fig. 64). They are in many respects similar to the ovaries but are hand-shaped, the broad end

of the hand being attached and the fingers free. Their ducts which convey away the spermatozoa are called the vasa efferentia. They have similar funnel-shaped openings to those of the oviducts and they traverse the septum behind the segment in which these openings lie, but they do not at once open to the exterior. The two ducts of each side unite in the twelfth segment, and the common duct thus formed runs back to open by a pore with swollen lips on the fifteenth segment, i.e. the one behind that on which the oviducts open (7, Fig. 64). It is termed the vas deferens.

Since both genital ducts and nephridia are tubes opening at the inner end into the coelom and at the other end to the exterior, it used to be supposed that they were the same kind of thing, in a word that the genital ducts were modified nephridia. The study of their development has proved that such is not the case. The genital duct arises as an outgrowth of the coelomic sac—it is therefore termed a coelomiduct. The nephridium is always an ingrowth from the ectoderm. The so-called nephridia of Mollusca are really modified coelomiducts, and are not comparable with the nephridia of Annelida. The ovaries of the earthworm lie freely in the body-cavity and can be seen readily if the intestine be removed, each pair of testes and the corresponding inner funnel-shaped openings of the vasa deferentia are concealed by a certain sac or bag called the vesicula seminalis, and it is only by cutting away the wall of this sac that these structures come into view (4, Fig. 64). Each vesicula seminalis is a flat, oblong bag extending backwards from the front wall of the segment in which it lies and situated beneath the alimentary canal. The angles of the front vesicula seminalis are produced into two long pouches which project upwards at the sides of the alimentary canal, and are often called lateral vesiculae seminales, though they ought to be termed lateral horns of the anterior vesicula seminalis. Similar projections are produced from the hinder angles of both of the anterior and of the posterior vesiculae seminales, so that on opening a worm three pairs of grayish white sacs are seen at the sides of the gut. The study of the way in which the vesicula seminalis is formed shows that the space it contains is really part of the coelom which has become cut off from the rest by the outgrowth of folds from the septa, so that, although at first sight the testes seem to differ from the ovaries and to be exceptions to the general rule that reproductive cells have their origin from the walls of the coelomic cavity, a closer examination shows that this apparent divergence is not a true one.

Every earthworm has grown up from an egg which has been fertilised by a spermatozöon. As the earthworm is hermaphrodite, that is to say, contains both male and female organs, it might be thought that the spermatozoa of an individual would fertilise its own ova, but this is not the case. Cross fertilisation or the fertilisation of the ova of one individual by the spermatozoa of another is the rule in Nature, and the earthworm is no exception to the rule. The method by which the spermatozoa reach the ova is not clear in all its details, but it is something like this. The cells which are to form the spermatozoa break off from the testes and whilst lying in the fluid contents of the vesicula seminalis they divide and the products of the division or spermatozoa develop each a long vibratile tail by whose aid they swim actively about. Two earthworms then approach each other and place their ventral surfaces in contact. The heads of the pair are turned in opposite directions. Since the ventral surfaces are slightly grooved a sort of tube is formed by the opposition of the two worms, and the pair are bound together by a mantle of slime secreted by the goblet cells. The spermatozoa of one of the pair, which acts as male in this embrace, pass down the sperm funnels and vasa deferentia into the tube formed by the adpressed ventral surfaces of the worms. The spermathecae of the one which acts as female are filled from this tube. The earthworms then separate, one carrying away the spermatozoa of the other

The spermathecae in which the earthworm stores up the spermatozoa received from another individual are pockets of the skin (1, Fig. 64). They belong, strictly speaking, to the female reproductive system. Seen from the interior of the animal, they appear as four small white spherical bodies, lying one pair near the hind end of segment nine, and the other pair near the hind end of segment ten, and each pair opens by a very short neck or duct on the grooves between segments nine and ten and ten and eleven, just inside the outer pair of chaetae. It is through these ducts that the spermatozoa from another worm enter.

Earthworms lay their eggs in cocoons, which at one time were mistaken for the eggs themselves. These cocoons are usually brown and horny and vary in size in different species of earthworm; some are about as large as rape seed, others almost equal in bulk to a small grain of wheat. They are formed from the secretions of the peculiar ectoderm cells found in the clitellum and at first have a ring-like shape. The secretions harden when in contact with the air. The animal begins to wriggle out of the band, which at first

surrounds its body in the neighbourhood of the thirty-second to the thirty-seventh segment. As the band passes over the openings of the oviducts in the fourteenth segment it carries away with it a certain number of ova, and as it passes the orifices of the spermathecae between the eleventh and tenth and tenth and ninth segments, some of the spermatozoa which have been received from another individual are squeezed out. Besides ova and spermatozoa the cocoon contains a certain amount of a milky and nutritive fluid in which these cells float; this is probably supplied by certain other glands in the skin of the earthworm. At the moment the last segment, that is, number one, is withdrawn, the anterior end of the cocoon contracts and closes, and as the posterior end of the band-like ring passes over the head it also closes, so that the cocoon lies in the earth as a closed vesicle containing eggs, spermatozoa and a nutritive fluid. The spermatozoa fuse with the ova and from the fertilised ova, by division into a number of cells and by the differentiation of the cells into muscle cells, epithelial cells, digestive cells, nerve cells, etc., a young earthworm is built up. Before being hatched out of the cocoons the young embryos are nourished by the milky nutritive fluid in which they float.

Species of Earthworm.

In Great Britain there are several species of earthworm, which are grouped into two genera, viz. *Allolobophora*, with fourteen species, which, with one exception, have the prostomium not dove-tailed into the peristomium; and *Lumbricus*, with five species, in which the prostomium is completely dove-tailed into the peristomium. The above account has been taken from the anatomy of *L. herculeus*, the largest of our indigenous species, but with the exception of a few minor details the account applies to most British earthworms.

Order I. **Oligochaeta.**

The sub-order to which earthworms belong, the Terricolae, are for the most part inhabitants of the land, and occur widely distributed over the earth, being, as a rule, only absent from sandy and desert soils. Some of them are aquatic but not many. On the other hand the allied sub-order the Limicolae are for the most part denizens of fresh water. A few Limicolae possess gills or finger-like processes well supplied with blood-vessels which take up oxygen from the surrounding water. Both sub-orders contain numerous genera and families; together they form the order Oligochaeta, which is characterised by being hermaphrodite, by

having the reproductive organs few in number and definite in position, by developing directly from the egg without the intervention of any larval stage, and lastly by the absence of certain structures which are very characteristic of the other great division of the true worms or Chaetopoda.

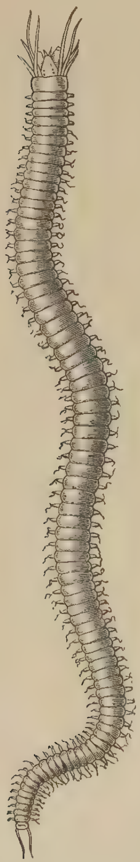

FIG. 65. *Nereis pelagica*, L. After Oersted.

Order II. **Polychaeta.**

The Polychaeta differ from the Oligochaeta, as their name implies, by possessing a large number of chaetae on each segment. The sides of each segment are further as a rule drawn out into hollow flaps or lobes called parapodia, which bear the chaetae. Each parapodium may be divided into a dorsal half, the notopodium, and a ventral half, the neuropodium (15 and 16, Fig. 66). Both notopodium and neuropodium carry bunches of chaetae, and each has as a rule one particularly large chaeta, the aciculum, completely concealed in a very deep chaeta-sac, which is moved by muscles attached to its base and serves as a kind of skeleton for the parapodium. There is usually above the notopodium and beneath the neuropodium a process called a cirrus. The dorsal cirrus may be modified into a gill, and both dorsal and ventral cirri are absent in some cases.

The coelom is often divided into three longitudinal compartments by two muscular partitions (5, Fig. 66) which run from the dorso-lateral line towards the median ventral line near the nerve-cord. The nephridia lie beneath these muscular partitions. It is of great interest to notice that in a few genera they do not terminate internally in a funnel which opens into the coelom but terminate like the nephridia of Platyhelminthes, Nemertinea and Rotifera in a group of flame-cells or solenocytes. The sexes are separated in Polychaeta, and the genital cells of each sex are developed from extensive stretches of the coelomic wall in every segment throughout a considerable region

of the hinder part of the body. Genital ducts in the form of wide ciliated funnels are likewise developed in many segments, but only acquire openings to the exterior at the time of sexual maturity. Sometimes they open into the tube of the nephridium. Such combinations of nephridium and coelomiduct have been called nephromyxia. The part of the animal containing the ripe sexual cells sometimes breaks off from the head end and floats at the surface of the sea. The head end may then grow a new series

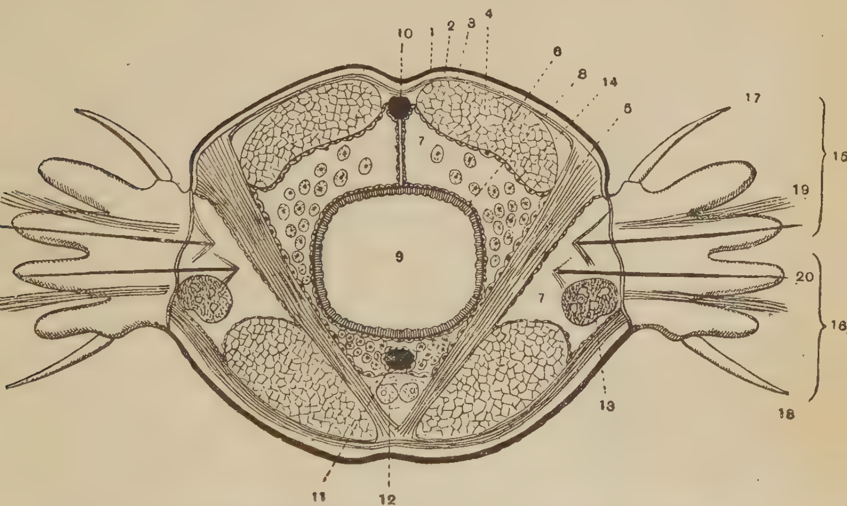

Fig. 66. Transverse section through *Nereis cultrifera*, slightly simplified. The parapodia are shown in perspective. Magnified.

1. Cuticle. 2. Epidermis. 3. Circular muscles. 4. Longitudinal muscles. 5. Oblique muscles forming a partition. 6. Parietal layer of epithelium. 7. Coelom. 8. Visceral layer of peritoneum. 9. Cavity of intestine. 10. Dorsal blood-vessel. 11. Ventral blood-vessel. 12. Ventral nerve-cord. 13. Nephridium cut in section. 14. Ova. 15. Notopodium. 16. Neuropodium. 17. Dorsal cirrus. 18. Ventral cirrus. 19. Chaetae. 20. Aciculum with muscles at inner end.

of hinder segments. The septa which divide the coelom in one segment from that in the next are in many forms incomplete or absent.

As a rule Polychaeta have a certain number of the anterior segments modified to form a head, which often carries tentacles; organs for absorbing oxygen from the water, called branchiae or gills are also often developed sometimes from the head sometimes from the middle region of the body. Polychaeta are generally

of separate sexes, and the eggs develop into a larva which swims in the sea and gradually changes and grows up into a worm. This group includes a very great variety of forms, almost all of which are marine. With few exceptions they form burrows for themselves, which most of them occasionally desert in order to seek prey and to discharge the reproductive cells. Some however never leave the burrows, which in this case often take the form of tubes composed of a secretion of the ectoderm.

FIG. 67. *Hirudo medicinalis*, about life size.

1. Mouth. 2. Posterior sucker. 3. Sensory papillae on the anterior annulus of each segment. The remaining four annuli which make up each true segment are indicated by the markings on the dorsal surface.

Order III. **Hirudinea.**

Besides the Oligochaeta and Polychaeta the order Hirudinea, the members of which are popularly known as leeches, is included amongst the Chaetopoda. They were for some time regarded as a distinct order of Annelida, since the great majority of species possess no chaetae and have other peculiarities; but the recent discovery of species possessing chaetae, and the close resemblance between the development of all Hirudinea and that of Oligochaeta, renders it evident that they are true Chaetopoda and that the absence of chaetae is a secondary characteristic.

Leeches. External features.

There is little doubt that the Hirudinea are closely allied to the Oligochaeta; indeed there are certain families which it is not easy to assign definitely to either group; but the more typical forms are easily distinguished. Externally leeches may be recognised by the possession of a sucker at each end of the body, the anterior one being formed by the mouth, whilst the posterior one is a special organ. By alternately attaching and releasing these suckers and bending the body the animal crawls along.

With the exception of *Branchellion*, which bears tufted gills, the bodies of leeches are without external processes. There are no parapodia, as in the Polychaeta, and no branchiae or tentacles, and only one genus of the family has any chaetae. The body is segmented, and recently it has been shown that the number of segments is always thirty-three. Some however of the segments are fused together; thus for example the posterior sucker contains traces of six or seven true segments. The best test of the number is to count the ganglia on the ventral nerve-cord. But even this is not decisive, because although there are twenty-one free ganglia in the centre of the body a certain number, some say five and some six, are fused into the first ventral ganglion, and a certain number, some say seven and some say six, coalesce to form the ganglion of the posterior sucker. Whichever view is taken the total number of segments is thirty-three.

The body of the leech is ringed or divided into a number of annuli. These do not, however, represent the segments, but a number, varying in the different genera, make up a segment. In *Hirudo*, the medicinal leech, there are five annuli to a true segment; in *Clepsine*, a common fresh-water leech, the number is three. The real segmentation is, however, to some extent indicated by markings on the skin.

The animal is covered like the earthworm by a thin cuticle secreted by the outermost cells, and the ectoderm contains numerous goblet cells which are especially well-developed over the segments abutting on the generative orifices. Here they form a clitellum, and the secretion which the goblet cells pour out forms a cocoon in which the eggs are laid.

Internal Organs.

The nervous system of a leech does not differ in essentials from that of the earthworm, but the nephridia, of which there are in *Hirudo* seventeen pairs, are peculiar. They are no doubt a modified form of the same organ as the nephridium of the earthworm, and they are best described as U-shaped rods of cells. One end of the U communicates with the exterior by a muscular vesicle; the other end is unconnected with anything else, but from the end connected with the muscular vesicle a delicate cord of cells proceeds inwards and terminates in a structure something like a minute cabbage situated in a sinus above the testis. This termination is called the testis lobe. The whole nephridium is traversed by a

ramifying network of chambers opening by minute pores on the testis lobe.

The other systems of organs are still more unlike what has been described in the case of the earthworm and deserve a short account. Leeches live by sucking the blood or juices of other animals, usually of Vertebrates. They are divided into two large groups—(*a*) the *RHYNCHOBDELLIDAE*, which pierce the tissues of their hosts by means of a fine protrusible stomodaeum, the so-called proboscis, and (*b*) the *GNATHOBDELLIDAE*, which bite their prey by means of horny jaws. The medicinal leech is one that bites, and the triradiate little scar which its three teeth make in the skin was well-known to our forefathers in the times of bleeding and cupping. The three teeth, which are notched like a saw, are really only thickenings of the cuticle borne by the wall of the pharynx, which contains many unicellular glands whose secretion prevents blood from coagulating. Thus the leech when fixed on to its victim by the oral sucker readily obtains a full meal.

From the pharynx a short narrow tube, the oesophagus, leads into an enormous dilatation, the crop. This extends to the fourteenth segment and gives off on each side a series of eleven pouches or caeca (Lat. *caecum*, blind) which increase in size from before backward. The posterior caeca are very large and reach back to the level of the anus, lying one on each side of the intestine. The leech has the habits of a boa-constrictor. It makes a hearty meal, absorbing as much as three times its own weight of blood, and the blood it absorbs is stored up for many months in this enormous crop. It slowly digests the food in a small globular stomach situated just behind where the posterior caeca leave the crop. The stomach opens into a short intestine which ends in the anus, a minute pore situated dorsally between the posterior sucker and the body (Fig. 68).

Coelom.

In one genus at least, *Acanthobdella*, the coelomic cavity is almost as well-developed as in an earthworm, and is divided up by septa as in that animal, but in other leeches the cavity tends to disappear, becoming in fact filled up by a great growth of tissue, and thus reduced to a few narrow channels. In many leeches it contains a fluid closely resembling the true blood, so that unless very careful microscopic examination be made these channels may be mistaken for true blood-vessels. The capsules in which the ovaries and testes lie are also parts of the coelom.

The medicinal leech, owing to a great growth of this above-mentioned tissue, is almost without a coelomic cavity. When the body is opened a narrow vessel full of a red fluid is seen running along the middle dorsal line above the alimentary canal. This is the dorsal sinus, a remnant of the true coelomic cavity; a similar sinus runs along the ventral surface underneath the alimentary canal, which is called the ventral sinus. It communicates with the dorsal sinus by lateral channels which run between the intestine and the posterior caeca of the crop. It surrounds the ventral nerve-cord, which thus seems to float in blood but really lies in the red coelomic fluid, and it gives off lateral sinuses which surround the inner openings of the nephridia. The true blood-vessels comprise a vessel running on each side of the body and connected together by transverse branches which run from side to side below the ventral sinus. These lateral vessels further supply capillaries to the nephridia, alimentary canal, reproductive organs, etc., and a very extensive system to the skin where the haemoglobin of the blood takes up oxygen. Except in *Branchellion*, which has special gills, the respiration of leeches is carried on by the skin.

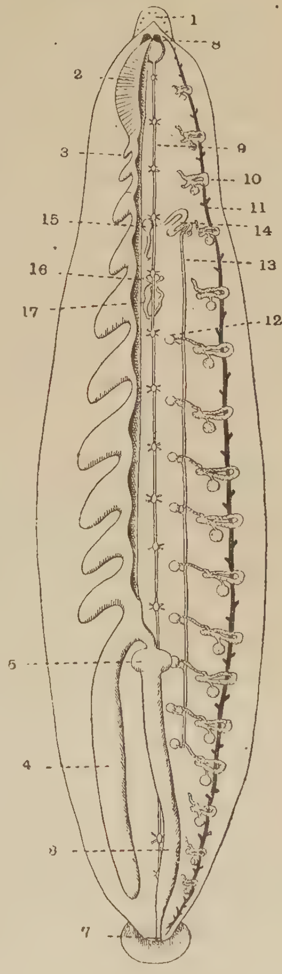

Fig. 68. View of the internal organs of *Hirudo medicinalis*. On the left side the alimentary canal is shown, but the right half of this organ has been removed to show the excretory and reproductive organs.

1. Head with eye spots. 2. Muscular pharynx. 3. 1st diverticulum of the crop. 4. 11th diverticulum of the crop. 5. Stomach. 6. Rectum. 7. Anus. 8. Cerebral ganglia. 9. Ventral nerve-cord. 10. Nephridium. 11. Lateral blood-vessel. 12. Testis. 13. Vas deferens. 14. Prostate gland. 15. Penis. 16. Ovary. 17. Uterus—a dilatation formed by the conjoined oviducts.

Reproduction.

Leeches are, like the earthworm, hermaphrodite, but their reproductive organs differ in some respects from those of that animal.

In *Lumbricus* the testes are repeated in two segments only, but in *Hirudo* there are usually nine pairs of testes. The cavities of both the testis and of the ovary are to be regarded as part of the original coelom; in strictness the testes probably correspond to the vesiculae seminales in an earthworm, which are part of the coelom, and enclose the true testis and the sperm-funnel. Each testicular sac produces spermatozoa on one side and on the other side is ciliated. The ciliated tract is the sperm-funnel and leads into a short transverse duct which passes into a longitudinal canal termed the vas deferens, there being one such canal on each side of the body. At its anterior end each vas deferens passes into a convoluted mass of tubes—the so-called epididymis—whose walls secrete a substance which binds the spermatozoa together into packets called spermatophores. From each epididymis a short duct passes towards the middle line, and these two ducts fuse and enter the base of the penis, which is protruded from the segment which contains the sixth distinct post-oral ganglion. The base of the penis is surrounded by glandular cells which discharge into it and which collectively are termed the prostate gland. They form a milky fluid in which the spermatophores are bathed. It is to be remembered that the names epididymis, prostate, etc., are given from fanciful resemblances to parts in the anatomy of man by no means homologous with the organs bearing the same name in the leech.

The penis is simply the muscular end of the conjoined male ducts or vasa deferentia; it is the organ by which the spermatophore is deposited in the body of another leech. The spermatozoa in *Clepsine* seem to penetrate the skin at any point and make their way to the ovaries, where they fertilise the eggs. In other species the spermatozoa enter in the usual way by the female genital pore.

As in the earthworm, there is but one pair of ovaries. These are minute filamentous bodies each enclosed in a small coelomic sac. From each sac a short oviduct proceeds and uniting with its fellow forms a twisted tube surrounded by many glands. This finally opens by a median pore on the segment behind the one bearing the male opening.

Thus in leeches, unlike the condition in the earthworm, the genital pores are single and median. The medicinal leech lays its eggs in a cocoon and buries them in holes in the banks of the

ponds it inhabits. *Clepsine*, one of the Rhynchobdellidae which is very common in Britain, attaches its eggs to some stone or water-plant, or in some species carries them about on its ventral surface. It has developed a quite maternal habit of brooding over the eggs, and when the young are hatched it carries them about and they feed on some secretion from its body.

Habits, etc.

Of the Gnathobdellidae, *Hirudo medicinalis* is found in Great Britain, but is commoner in some parts of the Continent. It is cultivated in some districts, but the demand for it is decreasing with the disappearance of blood-letting. It becomes mature in three years. In the young stages it sucks the juices of insects. Another common but small Gnathobdellid leech is the brownish *Nephelis*, which frequents our ponds and pools; it feeds on snails and planarians. A large species of the same genus is common in the shallows of the St Lawrence, in Canada. In warmer climates many leeches take to living on land, and are a source of great annoyance to travellers whose blood they suck. Even water-forms do much damage unless carefully guarded against. Certain species make their way with drinking water into the throat and back of the mouth, on which they fasten, and so cause great suffering both to man and cattle.

Phylum ANNELIDA.

This phylum includes segmented animals with, as a rule, a well-developed coelom and metamerically repeated nephridia. The cuticle is always thin and flexible, and the nervous system consists of a pair of supra-oesophageal ganglia, a nerve collar and a ventral nerve-cord which has a ganglionic swelling in each segment.

Class I. Chaetopoda.

Annelida which possess bristles (chaetae) embedded in pits in the skin and serving as organs of locomotion, or which are believed to have once possessed such organs and to have lost them.

Order 1. **Oligochaeta.**

Chaetopoda which have the chaetae arranged singly or in pairs and which have neither parapodia nor tentacles: the generative organs are definitely localised and the sexes are united in the same individual: development is practically entirely embryonic: the group inhabits fresh water or damp earth.

Ex. *Lumbricus, Allolobophora.*

Order 2. **Polychaeta.**

Chaetopoda which have the chaetae arranged in bundles of some size, almost always borne on conspicuous lateral outgrowths of the body termed parapodia: the prostomium has, as a rule, tactile organs, known as tentacles and palps: there are no localised generative organs, ova and spermatozoa being developed from wide stretches of the coelomic wall; the sexes are separate: in the development a well-marked larval stage occurs: with few exceptions the group is marine.

Ex. *Nereis.*

Order 3. **Hirudinea.**

Chaetopoda in which chaetae and parapodia are absent and which move by means of a muscular sucker developed on the under surface of the posterior segments: there are no tentacles and the mouth acts as an anterior sucker: the coelom is reduced to capsules surrounding the genital cells and to a few narrow channels: the animals are hermaphrodite, and the genital pores single and median: the members of this order live on the juices of other animals, and there are both fresh-water and marine species: development is entirely embryonic.

Sub-order 1. **Acanthobdellidae.**

Leeches which retain a few pairs of chaetae and have spacious coelomic cavities divided by septa.

Ex. *Acanthobdella.*

Sub-order 2. **Rhynchobdellidae.**

Leeches which have lost all chaetae and in which the coelom is reduced to a series of narrow channels. The stomodaeum can be everted and is termed a proboscis.

Ex. *Clepsine* (*Glossiphonia*).

Sub-order 3. **Gnathobdellidae.**

Leeches which have lost chaetae and have a reduced coelom. The stomodaeum is not eversible but forms a sucker provided with three thickened muscular ridges covered with rough cuticle which act as jaws.

Ex. *Hirudo*, *Nephelis.*

CHAPTER XI

PHYLUM GEPHYREA

In the older books of zoology under the head of Annelida a subdivision is included which is termed Gephyrea. The Gephyrea were defined as Annelida which had lost all signs of the metameric segmentation of the body and in which moreover the ventral nerve-cord is uniform in diameter throughout and in which there are no septa dividing successive coelomic cavities from one another. What remains of Annelid character is as follows: (1) The possession of a dorsal brain, nerve-collar and ventral nerve-cord. (2) The possession of a spacious body-cavity or coelom from whose walls, in the majority of cases, the genital cells are produced. (3) The possession of tubes opening to the exterior which in most cases combine the functions of excretory organs and genital ducts. The group used to be divided into Gephyrea nuda which burrowed in sand and mud, and Gephyrea tubicola which lived in clear water sheltered in leathery tubes secreted by the ectoderm. The Gephyrea nuda were further divided into (*a*) Armata, which possessed a smaller or larger number of chaetae embedded in the skin and which had an elongated praeoral lobe or prostomium, and into (*b*) Inermia which were devoid of chaetae and of prostomium, but in which the anterior part of the body could be turned outside in—or introverted like the finger of a glove.

Modern research seems to indicate that in the Gephyrea nuda we have confounded together three quite distinct groups whose connection with one another is more than doubtful. These are as follows: (1) The Echiuroidea which possess chaetae embedded in the skin, a much elongated, grooved and ciliated prostomium, and in which the anus is at the posterior end of the body. (2) The Sipunculoidea in which there is no prostomium, but in which the front part of the body can be introverted into the hinder part, and in which the anus is situated far forward on the dorsal surface of

the body. (3) The Priapuloidea which agree with the Sipunculoidea in having no prostomium and in having the front region of the body introversible, but in which the anus is terminal.

Now the development of Echiuroidea demonstrates that this group really does belong to the Annelida, for the larva is distinctly divided into segments and each segment contains a section of the coelom. Since they possess at least a pair of chaetae they are Chaetopoda, and since the generative cells are developed from the wall of the coelom covering the ventral blood-vessel along the whole length of the body, and since the same organs act as excretory organs and genital ducts, they are to be regarded as modified Polychaeta. They are in fact Polychaeta which have ceased to burrow and which pass their lives in one spot, feeding themselves by what is brought to them by the current of water produced by the cilia lining the under surface of the prostomium. In the genus *Bonellia*, which is found in the Mediterranean, the prostomium is produced at its anterior end into two muscular flaps which are used for seizing prey. The prostomium of *Bonellia* when fully extended is 10 to 15 times as long as the animal, and this is a remarkable instance of the way in which any organ of the body can be increased in size indefinitely by the action of natural selection if it becomes of importance in obtaining food for its possessor, for it must be remembered that the enormous "proboscis" of *Bonellia* is strictly comparable with the insignificant lobe which overhangs the mouth in the earthworm.

One striking peculiarity of the Echiuroidea may be mentioned and that is, that in addition to possessing anterior nephridia which serve as genital ducts, they likewise possess a pair of peculiar nephridia which open into the hindermost part of the alimentary canal. These terminate internally in a multitude of small ciliated funnels opening into the body-cavity These funnels are scattered all over the surface of the nephridia.

The Sipunculoidea are not closely connected with the Annelida. The features which they have in common with them are distinctive, not merely of Annelida but of a wide range of animals which retain the coelom in a more or less primitive condition, and these only show that both Annelida and Sipunculoidea belong to the Coelomate division of Metazoa. Since the line joining mouth and anus is to be looked upon as the dorsal surface, it follows that the main part of the length of these animals is to be regarded as being made up of a great protrusion of the ventral surface of the body. The same is

true of the Gephyrea tubicola and there are a great many other features in which the Gephyrea tubicola and the Sipunculoidea resemble one another. We may therefore with great plausibility regard these two groups as forming an independent group of animals or phylum for which the name Gephyrea may be reserved, the Echiuroidea being removed to the Polychaeta and the Priapuloidea being left on one side for the present as a completely isolated group until we know more about their development.

The Priapuloidea differ not only from the Sipunculoidea but from all the groups classed together as Gephyrea in the character of their excretory and genital organs. The genital organs are in the form of sacs, from the walls of which the ova and spermatozoa are produced, and which are directly continuous with the genital ducts, of which there are a pair opening to the right and left of the anus. When young specimens are examined no genital organs or genital ducts are to be found, but in their place two typical nephridia which end internally in a number of branches, each branch terminating in a flame-cell or solenocyte. As the animal grows, pouches are given off from the nephridial duct, the blind ends of which develop into the genital organs whilst the nephridial duct becomes the genital duct. Numerous specimens of the genus *Priapulus*, which has two branched gills protruding from the hinder part of the body, are found embedded in black mud in moderate depths in the Firth of Clyde.

The Gephyrea tubicola consist of a number of species which are grouped in a single genus *Phoronis*. The British species are minute creatures about $\frac{1}{6}$ of an inch long. The mouth is surrounded by hollow ciliated tentacles which spring from a lip or platform termed a lophophore, and this lophophore is not circular but drawn out at the side into two arms which project dorsally and give the whole the form of a horse-shoe. These tentacles are supplied with branches from dorsal and ventral blood-vessels and serve for respiration as well as to bring food. The anus is situated on the dorsal surface far forward and two ciliated funnels which serve both as genital ducts and excretory organs open at the sides of it. When *Phoronis* is young it swims about in the sea by means of an oblique ciliated band running behind the mouth and much resembles the larva of some Annelids. There is a large prostomium in the form of a hood overhanging the mouth and the anus is at the posterior end of the body. As the larva grows an intucking of the skin on the ventral surface makes its appearance. This becomes attached

to the intestine, and when the critical period of growth has arrived, the hood or prostomium is cast off: the ventral pouch becomes turned inside out and pulls out the intestine into a loop—and this everted pouch constitutes the greater part of the body of the *Phoronis*.

The largest of the Sipunculoidea is the species *Sipunculus nudus* which is found burrowing in the sand and mud in the Mediterranean. It is however used as a type for study by students of zoology in this country, and as species of the same genus occur on the American coast we may give a brief description of its anatomy and its habits. The animal is shaped somewhat like a sausage, and may attain a length of 10—11 inches and a diameter of nearly an inch. The front part of the body which can be retracted and which we may name the introvert is covered with minute papillae. The rest of the body is marked by a series of longitudinal grooves crossed by transverse ones so that the skin is divided into a series of squares. There is a well-developed cuticle somewhat loosely attached to the ectoderm beneath, and in the ectoderm are a series of glands, each of which consists of a number of oval cells arranged in the form of a shallow cup. The mouth is situated at the end of the introvert and is surrounded by what can only be described as a frilled membrane (*a*, fig. 69). This is represented in other genera by a horse-shoe of ciliated hollow tentacles lying dorsal to the mouth. This membrane is richly supplied with blood-vessels and seems to serve as gatherer of the minute particles of organic matter on which the animal feeds. The blood-vessels communicate with a main reservoir, the dorsal blood-vessel (*c*, fig. 69) which lies above the oesophagus. When blood passes from this into the membrane the latter becomes swollen out.

The animal burrows its way into muddy sand and feeds on it as well. If it is removed from the sand it turns and twists the introvert about, alternately retracting it and pushing it out until it finds sand of the proper consistency, when the introvert is driven in. It then becomes fixed in its new position by the appearance of a swelling on it immediately behind the mouth. It is then retracted and this action—since the introvert is fixed—necessarily draws the body after it. When the body is fixed the introvert is again extruded and so movement goes on.

When a *Sipunculus* is opened by a cut along the dorsal surface we find that we have cut into a spacious coelom undivided by any septum whatever. The most conspicuous organs which strike the

eye of the observer are the alimentary canal and four great retractor muscles of the introvert (*i*, fig. 69). These latter structures are arranged as a dorsal and ventral pair, they broaden out towards their posterior ends and are all inserted in the body-wall at the same distance from the mouth. Immediately behind the line of their insertion a slight thickening of the coelomic epithelium may be observed running round the body; this is the rudiment of the genital organ. From it in periods of genital ripeness the genital cells are produced and budded off into the coelomic cavity and float in the coelomic fluid. The alimentary canal runs back to the posterior end of the body, here it bends and runs forward to the anus. It is therefore bent in the form of a **U**, and the two limbs of the **U** are twisted round each other in a spiral fashion. From the recurrent or ascending limb of the **U** not very far from the anus there is given off a blind pouch (*j*, fig. 69). This pouch varies extraordinarily in length in different individuals, sometimes it is a mere vestige, sometimes it is half as long as the body. The walls of the alimentary canal are extremely thin, they can hardly be touched without rupturing them, and yet the canal is crammed with sharp fragments of shells and other débris, and it is extraordinary that these never seem to penetrate it. The thinness of the walls of the alimentary canal are probably in relation to the poor development of the blood-system, because though there are two blood-vessels on the dorsal side and one on the ventral side of the alimentary canal connected by a ring vessel immediately behind the mouth, yet they extend only a short distance backwards and their main function seems to be to expand the "frilled membrane" to which they give off numerous branches. The products of digestion must therefore diffuse directly into the coelomic fluid, and the effective mixing up of this is aided by the so-called "urns." These are cups of ciliated cells which are formed on the coelomic wall where it covers the dorsal blood-vessel and are budded off into the fluid.

The organs which function both as kidneys and as excretory ducts are a pair of so-called "brown tubes," which lie beneath the alimentary canal and open on the ventral surface some little distance behind the end of the introvert (*h*, fig. 69). They receive their name from the colour of the pigment (probably excretory) in their walls. They may be described as blind pouches, with however a lateral ciliated opening leading into the body-cavity and situated near the external opening. They much resemble the "anterior

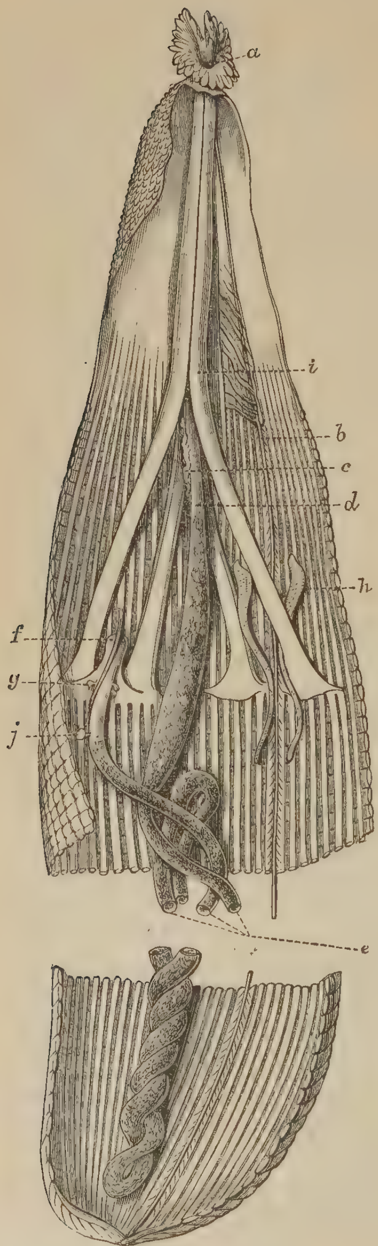

Fig. 69. Dissection of *Sipunculus nudus*.

a. Frilled membrane surrounding the mouth.
b. Ventral nerve-cord.
c. Dorsal blood-vessel.
d. Oesophagus.
e. Cut ends of the intestinal coil.
f. Anus.
g. Bush-bodies.
h. Brown tube.
i. Retractor muscle.
j. Blind pouch or caecum.

nephridia" of Echiuroidea, and this was one excuse for including the latter among Gephyrea. Attached to the sides of the intestine near the anus are two branched outgrowths termed bush-bodies. These (*g*, fig. 69) were formerly compared to the posterior nephridia of Echiuroidea; but they have been shown to be thickenings of the visceral peritoneum whence floating cells (amoebocytes) are budded off into the coelomic fluid.

The nervous system consists of a small squarish supra-oesophageal ganglion or brain which is beset by a number of curious lobes called fungiform processes. Above the brain there is a ciliated canal leading up to the external surface of the body—this is doubtless sensory in character. The ventral nerve-cord (*b*, fig. 69) shows no ganglionic thickenings of any kind, it is connected with the brain by a long "nerve-collar" which runs through the whole length of the introvert. In order to avoid the risk of straining these delicate cords when the introvert is suddenly shot out they are flanked on either side by a special muscle which takes the strain when the introvert is stretched.

The larva of *Sipunculus* in many ways resembles that of *Phoronis*. As in the latter larva, an oblique postoral band of cilia is the chief organ of locomotion. There is also as in the *Phoronis* larva a praeoral lobe, the greater part of which is eventually cast off. The anus is at first terminal but becomes slowly displaced on to the dorsal surface by the outgrowth of a ventral protrusion, so that what takes place with cataclysmal suddenness in *Phoronis* is effected by a gradual process in *Sipunculus*. The study of development therefore reinforces the arguments drawn from the study of adult anatomy that the two groups of Sipunculoidea and Phoronidea are akin, and it would be a great advantage if the old term Gephyrea were exclusively devoted to them.

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CHAPTER XII

PHYLUM ARTHROPODA

One of the most striking features of the Annelida is the fact that they are segmented, that is to say their body is divided into a number of similar parts placed one behind the other like coaches in a train, each of which to a greater or less extent resembles the part in front of it. The likeness of the parts to one another varies. In some worms we might easily detect from which region of the body any given segment was taken. In the Earthworm we found, that, except in the region of the clitellum, there is little external difference; nevertheless if we consider the internal organs we can distinguish any of the first twenty segments from any other behind these and can easily arrange them in their proper order; but no matter how long the worm is, all the segments behind the twentieth resemble one another so closely that it is impossible to assign any to their right place, except the last of all (*v.* p. 142).

Arthropoda. The animals included in the group of the Arthropoda are segmented like the Annelida, but with few exceptions the number of segments is small and does not exceed twenty. The segments have also become more highly differentiated from one another in consequence of being modified to perform various functions, and they are more frequently fused together than is the case in the Annelids.

The Arthropoda have jointed outgrowths called limbs or appendages. These are always arranged in pairs, and almost always at least one pair is modified so as to assist in holding and crushing the food. These modified limbs are termed gnathites (Gr. *γνάθος*, jaw). This character of possessing jointed limbs is what is indicated by the name Arthropoda (Gr. *ἄρθρον*, joint; *πούς*, foot).

The strength of these outgrowths lies in the thickness of the cuticle secreted by the ectoderm surrounding them. The thickness of the cuticle which constitutes the exoskeleton is the distinguishing feature of all Arthropoda.

The exoskeleton not only furnishes an external armour but penetrates between the limbs of inturned folds of ectoderm termed apodemes into the interior of the body and furnishes support for the muscles.

Classification.

The Arthropoda may be divided into the following classes:

I. The CRUSTACEA, possessing two pairs of feelers (antennules and antennae) and three pairs of jaws—which include all the Crabs, Lobsters, Crayfish, Barnacles, Wood-lice, etc., besides countless small forms such as the Water-flea, *Cyclops*, and many others which inhabit both salt and fresh water.

II. The ANTENNATA, which include all Arthropoda possessing one pair of feelers—antennae—and breathing by means of air tubes or tracheae. This group is divided into three sub-classes, viz.:

A. The Prototracheata, a group containing the genus *Peripatus*, an animal not found in Europe or in North America, but which must be mentioned because it seems to be a survival from an earlier age and because its structure has given us a clue to much that was obscure in the anatomy of Arthropods; it is in fact in many respects intermediate between the Annelids and the air-breathing Arthropoda.

B. The Myriapoda or Centipedes, the commonest British examples of which are the chestnut-coloured centipede *Lithobius forficatus* and the black "wire-worm[1]" *Iulus terrestris*.

C. The Insecta, the largest group in the Animal Kingdom. It contains about 250,000 named species, and includes all those creatures such as Beetles, Flies, Dragon-flies, May-flies, Moths, Bees, Ants, Wasps, etc., which we are accustomed to call insects.

III. The ARACHNIDA, devoid of feelers but having a small pair of claws (chelicerae) as first appendages, and having as jaws mere processes of their walking legs. This class includes the Spiders, Harvestmen, Mites and certain larger forms such as the Scorpion, and *Limulus*, the King-crab.

IV. The PANTOPODA, with chelicerae but devoid of jaws altogether, a group of small animals incorrectly termed "sea-spiders." They are marine and may be found under stones between tide marks on our coast.

V. The TARDIGRADA or "Bear Animalcules." These are minute microscopic Arthropoda found amongst moss and decaying

[1] This is not to be confused with the larva of a beetle, *Elater lineatus*, which is also called a "wire-worm" by the British agriculturist.

vegetation. They have a few pairs of stumpy legs each ending in two claws. They are devoid of antennae, jaws and chelicerae.

In order to get a clear and definite idea of the structure of the Arthropoda we shall select for closer examination the common fresh-water Crayfish which belongs to the class Crustacea. This in England is *Astacus fluviatilis*, an animal which when full grown is six inches long, but in America the "common" crayfish is represented by various species of the allied genus *Cambarus*: the common denizen of the St Lawrence is *Cambarus virilis*, a smaller and more slender creature than the English crayfish, not exceeding five inches in length. The crayfish looked at from above is seen to be composed of a nearly cylindrical anterior portion—the cephalo-thorax and a hinder more flattened portion divided by constrictions into a series of similar rings placed one behind the other and at once recalling the segments of an earthworm. This jointed portion is called the abdomen. The cephalo-thorax is covered above by a hard horny skeleton called the carapace (*c*, fig. 70) and the rings of the abdomen are similarly covered by pieces of a similar skeleton which are called terga. Close inspection shows that a similar though thinner covering extends over the joints between the cephalo-thorax and the abdomen and between the various rings of the abdomen—in fact the whole body of the crayfish has a continuous covering of horny matter, thin in some places, thick in others, which is to be regarded as an exaggeration of the cuticle found in the worm. The same is true of all Arthropoda and to this circumstance may be traced directly or indirectly most of the characteristics of the phylum. The thick pieces of the skeleton are known as sclerites and the thin flexible portions which permit of the movement of one sclerite on the other are termed arthrodial membranes.

Each segment of the abdomen has a pair of outgrowths movably articulated with it called appendages. These differ from the parapodia of Polychaeta chiefly in being flexible only at certain places, and in being on the whole of simpler form. Like the typical parapodium, each consists of a basal piece and two forks, an outer or dorsal called the exopodite and an inner or ventral called the endopodite. The basal piece is called the protopodite. As compared with the parapodia of a worm the appendages spring more from the ventral surface and less from the sides, and hence the dorsal branch of the parapodium corresponds to the outer branch of the limb.

The ventral surface of the segment is protected by a narrow sclerite called the sternum and between successive sterna there are

broad intersternal arthrodial (*i.s*, Fig. 71) membranes which permit of a great amount of downward bending of the abdomen, for in such a movement they must of necessity be much puckered. On

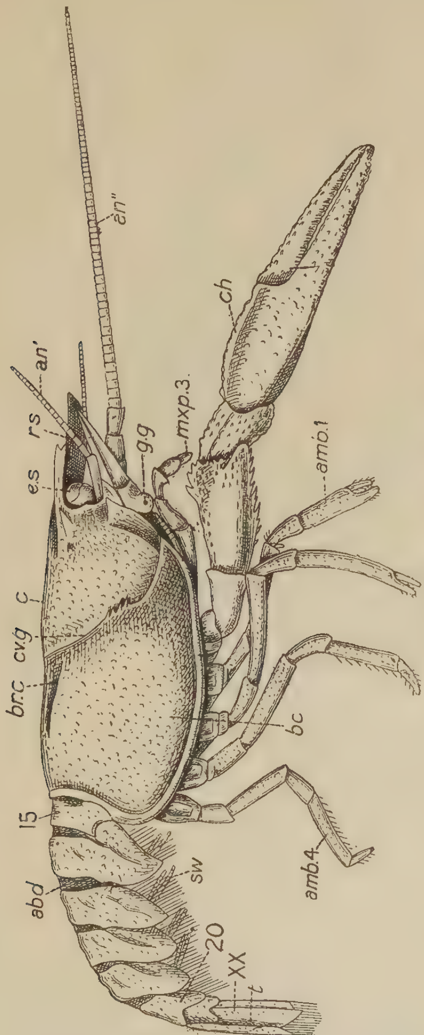


FIG. 70. The common Crayfish, *Astacus fluviatilis*, seen from the side.

abd. Abdomen. *amb.* 1. First walking leg. *amb.* 4. Fourth walking leg. *an'*. First antenna or antennule. *an''*. Second antenna. *bc.* Branchiostegite. *br.c.* Branchiocardiac groove. *c.* Carapace. *ch.* Chela. *cv.g.* Cervical groove. *e.s.* Eye-stalks. *g.g.* Opening of green gland. *mxp.* 3. Third maxillipede. *rs.* Rostrum. *sw.* Swimmerets. *t.* Telson. 15. First segment of abdomen. 20. Last segment of abdomen. xx. The last appendage.

the outer side of the insertion of the limb there is a short sclerite running to the tergum, called the epimeron. The bent down edge of the tergum is distinguished as the pleuron but there is no line of demarcation between it and the rest of the tergum.

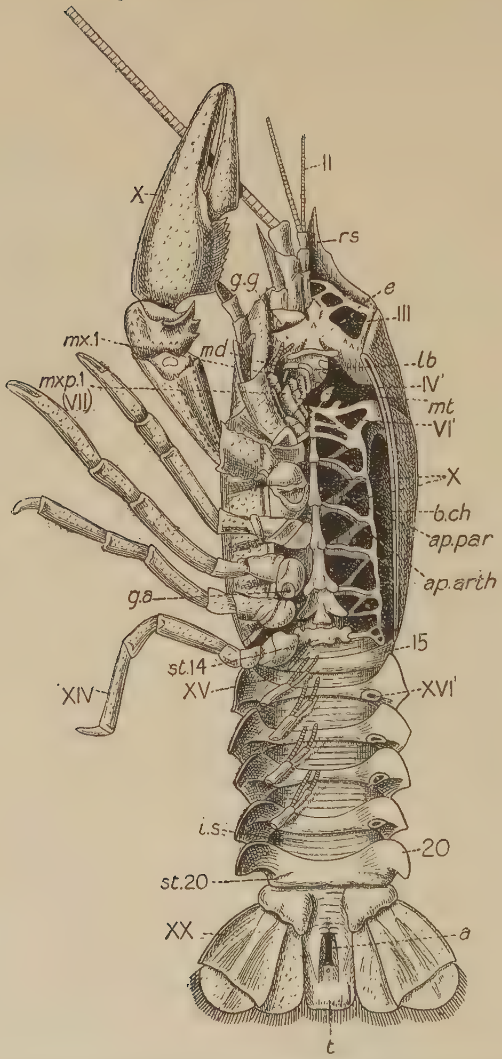


FIG. 71. *Astacus fluviatilis*, viewed from beneath. The appendages on one side have been removed.

a. Anus. *ap.arth.* Arthrodial apodeme. *ap.par.* Paraphragmal apodeme. *b.ch.* Branchial chamber. *e.* Epistome. *g.a.* Female genital aperture. *g.g.* Opening of the green gland. *i.s.* Intersternal membrane. *lb.* Labrum. *md.* Mandible. *mt.* Metastoma. *mx.*1. First maxilla. *mxp.*1. The first maxillipede. *rs.* Rostrum. *st.*14, *st.*20. The fourteenth and twentieth sterna respectively. *t.* Telson. Arabic figures denote the segments, Roman figures the appendages.

When the abdomen is bent upwards each tergum is found to articulate with both its successor and predecessor by two points situated one at each side. Each tergum slides to a certain extent under its predecessor: and each has a smooth part called the tergal facet, over which its successor slides.

The last division of the abdomen is a flat semicircular piece without appendages, which is divided into two by a transverse joint and on the under surface of which the anus is situated. This is called the telson, and in the lower Crustacea it is represented by a pair of appendages called the caudal fork between which the anus lies—it is believed that in the crayfish these appendages have coalesced to form the telson. The last regular segment bears a pair of appendages, both forks of which—exopodite and endopodite—have taken on the form of broad triangular valves (xx, Fig. 71). These can be folded the one under the other and the whole limb can be concealed under the telson but they can also be spread out at the sides of the animal's body so as to make with the telson a broad terminal fan.

By means of this fan the animal is able to execute a manoeuvre which is of the utmost value to it when it is pursued by its enemies. It bends the abdomen quickly and sharply downwards, striking the water with the outstretched fan and the reaction of the water drives the whole animal suddenly backwards. In this way the crayfish can *back* into a crevice between stones, whilst keeping its eyes fixed on its enemy.

In the case of the next three segments of the abdomen—the protopodite is composed of a stout cylindrical sclerite. Both exopodite and endopodite on the contrary are made up of a large number of short disc-like joints, so that these divisions of the limb are exceedingly flexible. They are furthermore fringed with "hairs," that is to say delicate spines of cuticle in no way comparable to the structures called hairs in Mammalia (see p. 636). It is instructive to notice the contrast between these structures and the chaetae of Chaetopoda. The Chaetae as we have seen are solid pillars of cuticle in which the oldest part is the tip. The "hairs" are on the contrary hollow structures containing at first an axis of ectoderm. The term seta has been proposed for them, and it is preferable to hair as the latter term suggests a false comparison.

The appendages under discussion—those belonging to the third, fourth and fifth segments of the abdomen—are termed swimmerets (*sw*, Fig. 70) and are much better developed in some of the lower

Crustacea, such as the Shrimps, and by means of them the animal is enabled to swim forwards. The crayfish is too bulky to be completely supported by the action of these appendages but when the crayfish creeps forwards by means of its other appendages, these by their vigorous motion support the abdomen and prevent it from resting on the ground, and aid the whole forward movement.

The appendages borne by the first two segments of the abdomen are obviously constructed on the same plan as those borne by the other segments but they have undergone great modification. From the fact that they differ greatly in the two sexes we should be led to suspect what proves to be the case, that this modification has taken place in consequence of their being used in connection with the sexual function. As is often the case with sexual appendages they vary much in shape from species to species and hence are of great value in classifying crayfish. In the male of *Cambarus virilis* the endopodite of the appendage belonging to the second segment is in its basal portion transformed into a rigid unjointed rod, whilst the endopodite of the appendage belonging to the first segment is transformed throughout its whole extent except the extreme tip into a grooved rod, whilst the exopodite is completely absent. When the appendages of the two segments are pressed together a tube is formed by the juxtaposition of the endopodites on each side, and through this tube the germ cells of the male are conveyed to the female. In the female the appendages of the second segment are like those of the third, fourth and fifth, whilst the appendages of the first segment are reduced to tiny vestiges.

Turning now to the carapace which covers the cephalothorax we find that it is divided into an anterior and a posterior portion by the cervical groove (*cv.g*, Fig. 70), a well marked transverse groove which crosses it. The portion of the animal in front of this groove is termed the head, whilst the part behind is called the thorax. The thorax is marked by two longitudinal grooves which, starting from the cervical groove run backwards to the hinder edge of the carapace. The two grooves are termed branchiocardiac grooves (*br.c*, Fig. 70) and the lateral areas marked off by them are known as the branchiostegites or gill-covers (Gr. *βράγχια* gills, *στέγειν* to cover) (*bc*, Fig. 70) and do not really form the lateral walls of the body but form two flaps which project at the sides and between which and the body the gills are lodged.

If we examine the under-side of the thorax we observe that it bears a number of long jointed appendages, between the bases of

which a series of very short sclerites are situated, which quite evidently correspond to the sternites of the abdomen. Hence we conclude—and the conclusion is confirmed by a study of the allies of the crayfish—that the thorax is composed of a number of segments like those constituting the abdomen which have secondarily become fused with one another through the thickening of the arthrodial membranes. The appendages above-mentioned differ in many respects from those of the abdomen. To begin with they are not forked, they consist of a limited number of exceedingly stout joints, and they are very much longer than those attached to the abdomen. It is usual to speak of them as legs, distinguishing the appendages of the abdomen as swimmerets. If we select for careful examination the last leg we find that it consists of 7 segments which are named, in the order proceeding from the base to the apex of the limb, coxopodite, basipodite, ischiopodite, meropodite, carpopodite, propodite, dactylopodite. Many of these names are suggested by fanciful analogies with the divisions of the human limb as the prefixes—cox- (Lat. *coxa* thigh), dactyl- (Gr. δάκτυλος finger) and others testify. It is indeed becoming usual to employ the English words wrist, hand and finger, for carpopodite, propodite and dactylopodite respectively, but it must be remembered that there is no real correspondence between the parts of the arthropodan and the human limb. From a comparison with the more anterior limbs of the crayfish it appears that the coxopodite and basipodite represent the protopodite of the swimmeret and the remaining five joints correspond to the endopodite. The dactylopodite or "finger" is a sharp-pointed segment. On the coxopodite of the last leg there is found in the male a small round opening. This is the aperture of the male genital duct and through it the male germ cells are shed into the tube formed by the first two appendages of the abdomen. Proceeding forwards in our examination of the appendages we find that the next leg is in all respects similar to the one described, but the three preceding legs are distinguished by the fact that each terminates in a claw.

This claw is due to a simple modification of the two terminal joints. The hand (propodite) is prolonged into a stiff spine which with the finger (dactylopodite) constitutes a pair of pincers. Of the three legs terminating thus, the first is by far the largest and strongest and has the joints constituting the claw very much enlarged. It is termed the chela, and it is the organ by which the crayfish obtains its food and defends itself against its enemies.

In order to give the chela rather more rigidity than the other

legs possess, the basipodite and ischiopodite are fused into one segment: this is effected simply by the thickening of the cuticle covering the arthrodial membrane between the two segments mentioned so as to destroy its flexibility. The crayfish feeds on any small animals that it can catch, it seizes water-snails for instance—dragging them out of their shells and tearing them to pieces with its chelae, and also greedily seizes on any dead fish it may come across.

The chela is the first of the long leg-like appendages of the animal, and as of these there are in all 5 pairs, the crayfish is said to be a Ten-footed Crustacean and to belong to the order Decapoda (Gr. δέκα ten, πούς foot).

The remaining 8 legs are used to enable the animal to creep cautiously forward, the abdomen being supported by the vigorous action of the swimmerets.

On the coxopodite of the third claw-bearing leg there is in the female a small round opening which is the aperture of the oviduct.

In front of the chela there are still to be found three pairs of appendages attached to the thorax but these are very much shorter than the "legs" and diminish rapidly in size as we proceed forward, so that the hindermost entirely conceals the rest. These appendages are termed maxillipedes which literally means foot-jaws (Lat. *maxilla* jaw, *pes* foot); this name was given to them because they were supposed to be intermediate in character between the other limbs and the jaws. This is true, but all the jaws of the crayfish are, as we shall see directly, modified limbs, hence the term foot-jaw is not distinctive. The maxillipedes might with propriety be termed "secondary jaws" for the corresponding limbs in the lower Crustacea have no resemblance to jaws and hence we conclude that the maxillipedes have only recently been modified in this direction, and may be expected to show still the first stages of the change. This indeed proves to be the case. If we examine the third and hindermost maxillipede we can see that it consists of exactly the same segments as the other thoracic limbs, but that the ischiopodite and basipodite are each prolonged inwardly into a sharp edge, so that when the two limbs of opposite sides are brought into contact in the middle line, the sharp edges mentioned above act like the cutting parts of a pair of nut-crackers. The meropodite and the "wrist," "hand" and "finger" are smaller in proportion to the ischiopodite than is the case with the corresponding segments of the limbs behind, so that we see that the first step towards converting a leg into a jaw is to

develop sharp cutting edges on the basal segments and to diminish the size of the distal segments. The cutting edges are termed gnathobases. This change becomes more and more marked as we proceed forwards. Thus in the second maxillipede the distal joints are reduced to three (the finger being absent) and the ischiopodite is as long as all three put together and finally in the first maxillipede the basipodite and coxopodite are greatly enlarged and produced

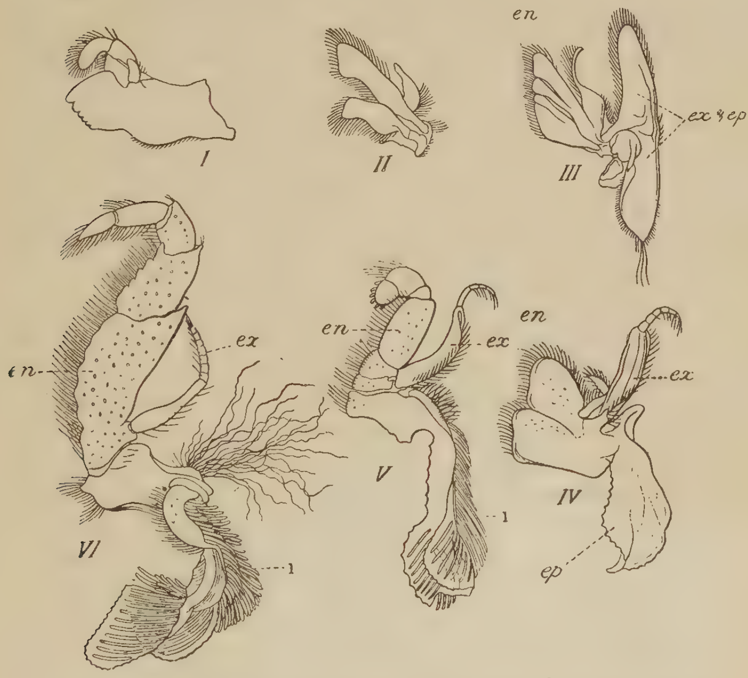


FIG. 72. Left mouth appendages of *Astacus fluviatilis*, slightly magnified. The other appendages are shown in Fig. 73.

I. Mandible. II. First maxilla. III. Second maxilla (Scaphognathite). IV. First maxilliped. V. Second maxilliped. VI. Third maxilliped. *en.* Endopodite. *ex.* Exopodite. *ep.* Epipodite. *ex & ep.* Scaphognathite, i.e. enlarged exopodite which in III forms a scoop for circulating water over the gills.

into cutting edges (gnathobases) and the whole endopodite is reduced to two tiny segments, which, taken together, are not as long as the basipodite.

A remarkable feature about the maxillipedes is that they each possess a well developed exopodite in the form of a whip-like filament

springing from the basipodite. We thus possess in the third maxillipede an exactly intermediate link between the swimmeret and the "leg," for it resembles the former in its forked character and the latter in the segments into which the endopodite is divided. Since in the lower Crustacea the forked type of limb is the rule we have every reason for supposing that the "legs" once had an exopodite which they have lost and indeed in one family of Shrimps vestigial exopodites are found, and so we regard the third maxillipede as the typical limb of the crayfish, from which by modification all the other types have been derived. The use of the exopodites will be pointed out when the respiration of the crayfish is described.

Turning now to the head region we find that it is covered by the carapace, an unjointed shield, which closely invests it above and at the sides and is produced in front into a pointed spine called the rostrum (*rs*, Fig. 70). The shape of this spine is a useful mark in discriminating one species from another. At its base on either side is a curved indentation—the eye-socket or orbit, from which the eye springs. The shield which covers the back of the thorax and forms the branchiostegites is a direct prolongation of the covering of the head. When we examine the corresponding parts of the body in the lower Crustacea we find that from the head there projects backward a large free fold of skin covering the thorax on the back and sides but not in any way adherent to it, and the segments of the thorax are freely movable like those of the abdomen. Hence we conclude that in the crayfish a similar outgrowth of the head region exists but that it has become adherent to the thorax along the mid-dorsal line whilst still projecting freely at the sides.

On the under side of the head there are two sterna in front of the mouth—the first excessively narrow, the second broader and termed the epistome (*e*, Fig. 71). These sterna are immovably fixed to one another and to the upper lip. This last is termed the labrum (*lb*, Fig. 71); it is a curved bar overhanging the mouth which has the shape of a longitudinal slit. Behind the mouth are two small lobes termed the metastoma (*mt*, Fig. 71) and at the sides of the mouth the head bears three pairs of appendages—which are modified so as to form jaws, making with the maxillipedes six pairs of jaws altogether. The hindermost of these is called the second maxilla or simply the maxilla. It is a thin and blade-like limb not unlike the first maxillipede in front of which it lies. The two segments of the protopodite, the basipodite and the coxopodite are each produced into gnathobases fringed with small spines, the

endopodite is a short unjointed filament whilst the exopodite is a broad jaw-like plate called the scaphognathite.

The first maxilla or maxillula is a still slenderer limb than the second maxilla—the exopodite is absent and the endopodite represented by a tiny filament, whilst from the basal joints two gnathobases are developed. The foremost of the three jaws is termed the mandible. It is much stronger and thicker than any of the jaws described except the third maxillipede, though in general form it recalls the first maxilla. There is one strong toothed gnathobase which has two edges, an outer cutting or "incisor" edge and an inner crushing or "molar edge," the exopodite is absent and the endopodite is a two-jointed appendage—much smaller than the gnathobase, which is termed the palp.

We can now form to ourselves some idea of the process of mastication in the crayfish. The flesh of the prey is torn into fragments by the chelae; these are then passed to the third maxillipede and then gradually worked forward through the whole series of jaws, becoming broken into finer and finer fragments before entering the mouth. The delicate maxillae appear to act like combs, removing the softer particles from the more resistant ones—these last being finally ground up by the stronger mandibles.

In front of the mouth there are to be found two pairs of appendages which are modified to act as feelers, and by means of these the crayfish explores the neighbouring water. These are the first and second pairs of antennae, the first pair being sometimes termed antennules (*an′*, Fig. 70) whilst the phrase antenna without qualification denotes the second pair (*an″*, Fig. 70). These appendages are proved by a study of development to have originally belonged to the region behind the mouth and to have been gradually shifted forwards during the course of growth. It is characteristic of Crustacea as distinguished from the other Arthropoda that they have two pairs of appendages in front of the mouth acting as feelers. The second or large antenna commences by a protopodite consisting of the usual two joints which are very short and broad. On the under surface of the coxopodite is a rather conspicuous knob of cuticle the summit of which is pierced by a hole. This is the opening of the kidney (*g.g*, Figs. 70 and 71). The exopodite is represented by a flat oblong scale—the squame—which is freely movable on the protopodite and which serves as a floor to the eye-socket. The endopodite is represented by a long filament two thirds the length of the body, the basal joints of which are stout and fairly long but the distal joints are disc shaped, so that the whole is exceedingly

flexible. Armed with this long antenna the crayfish explores the width and extent of the various nooks and crannies amongst the stones in the river bed in which he hides himself.

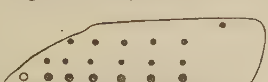
The first antenna or antennule is a much smaller organ. The protopodite consists of *three* stout joints, *not* two, as is the case with the thoracic protopodites, and hence we cannot label any of them basipodite or coxopodite. On the upper surface of the most proximal is an open pit the entrance to which is guarded by a fringe of branched setae. This is the otocyst or rudimentary ear, the structure and function of which will be explained later. Both exopodite and endopodite have the form of flexible filaments made up of a multitude of joints, the exopodite being by a little the longer and attaining about half the length of the head. On the under surface of each of its joints are two tufts of fine setae which are flattened and the tips of which are obtuse. These are believed to be olfactory in function so that the senses of smell and hearing are situated in the antennule. If a crayfish be watched when at rest it will be noticed that the antennules are in constant movement; the animal twitches them first in one direction and then in another. If now a piece of somewhat stale fish be dropped into the water near the animal, in a little while as soon as the odour therefrom has had time to diffuse, the twitching becomes much more violent and is now confined to the vertical plane joining the animal and the food and soon the crayfish creeps forward and secures the tasty morsel. It appears therefore that the animal not only perceives odours by means of the antennule, but by moving it about is able to discover the direction from which the odour has emanated.

In front of the first antennae are situated the eyes which form the summits of two short unjointed stalks freely movable on the carapace. Whether the eye-stalks are to be regarded as appendages comparable with the others is a disputed question. In the time of Huxley it was regarded as self-evident that they were appendages. Later when due weight was given to the facts that in many of the lower Crustacea the eyes are mere convex areas of the carapace, and that in none of them are the eye-stalks movable, it was considered more probable that the eye-stalks were simply portions of the carapace which had become movable to enable the eyes to have a wider range of vision. The study of development has however shown that the absence of an eye-stalk is a secondary condition of affairs and the remarkable fact that in some Shrimps when the eye-stalk with its contained optic ganglion is torn out, an

antenna-like organ grows in its place, suggests that after all the eye-stalk may be an appendage which we might perhaps compare to the "antennae" on the prostomium of a Polychaete worm.

The crayfish like all Crustacea is primarily adapted to a water-breathing life, though like many members of its class it is able to pass short periods out of the water if its respiratory organs be kept moist. These organs are feathery outgrowths of the body and limbs termed gills or branchiae. By cutting away the branchiostegite of one side the structure and arrangement of these organs can be observed. Commencing behind we find in the English crayfish (*Astacus fluviatilis*) a small gill springing from the thin side-wall of the thorax high above the insertion of the last leg. This gill, from its place of origin termed a pleurobranch (Gr. πλευρόν side), is absent in the species of *Cambarus*. It has the form of a filamentous stem beset with small flattened branches on all sides, through the thin walls of which the oxygen dissolved in the water diffuses inwards to the blood.

Proceeding forwards we find above the other thoracic legs no pleurobranchs (though in the Crabs [Brachyura] there is quite a series of them), but attached to the arthrodial membrane which connects the fourth leg to the body there are two gills, one placed above the other, which from their position may be termed arthrobranchs. These gills are similar in structure to the pleurobranch, but there is in addition a gill attached to the coxopodite of the limb, of rather a different structure. It commences in a circular basal plate from which springs a flattened stem called the lamina beset with two series of branches. This gill is termed a podobranch because it springs from the limb itself.

The 4th, 3rd, and 2nd legs, the chela or 1st leg and the third maxillipede have each attached to their bases and arthrodial membranes, a podobranch and two arthrobranchs, the second maxillipede has only a podobranch and the lower arthrobranch, whilst attached to the base of the first maxillipede there is a structure called an epipodite, which is a lamina devoid of gill filaments and must be regarded as a rudimentary gill. Hence if we construct a chart showing the arrangement of the gills of the English crayfish, we find remains of four parallel series of gills . The extent to which each series is developed really depends on the shape of the branchial cavity,

that is, the space enclosed between the branchiostegite and the side walls of the thorax. Thus as mentioned above, the Crabs having a high branchial chamber of shorter length than that of the crayfish have preserved more of the pleurobranchs and lost more of the podobranchs.

In order that the gills may be able to carry out their functions properly the water which bathes them must be constantly changed. In other phyla of the animal kingdom, notably the Mollusca, this is effected by means of cilia—but cilia are an impossibility to an Arthropod since the ectoderm everywhere seems to have an irresistible proclivity to produce cuticle.

In the absence of cilia a current of water is caused to pass over the gills by the action of the scaphognathite, that is, the exopodite of the second maxilla. This is a fan-shaped plate fitting into the extreme front corner of the branchial chamber. During the life of the animal it is in constant vibration, and it literally bales the water out of the front end of the branchial chamber, causing a current of fresh water to enter the hinder and lower end of the chamber between the edge of the branchiostegite and the bases of the legs. The whip-like exopodites of the maxillipedes aid the scaphognathite; they whisk away from the sides of the animal the water which the scaphognathite has baled out. The constant shaking of the gills in consequence of the motion of the legs must aid in ridding them of the film of water which might cling to their surfaces.

Turning now to the internal anatomy, if the carapace be clipped away from the mid-dorsal region of the head and the thorax, and the terga removed from the segments of the abdomen, a general view of the internal organs will be obtained. In the extreme front is seen the brain at the sides of which two roundish glandular masses, the kidneys, are situated: behind these the so-called "stomach" with its attached muscles. Behind the stomach we find the heart floating in a sac termed the pericardium, whilst in the abdomen we find a mass of muscle which, as we approach the pericardium, breaks up into strands which are attached to the sides of the thorax.

Although the heart and its vessels are the structures which naturally present themselves first on commencing dissection, yet it will be more convenient to describe the alimentary canal first of all. This canal differs sharply from the type found in most other groups of animals in the large part of its length which is constituted by the stomodaeum and the proctodaeum. The part lined by

endoderm is reduced to exceedingly small dimensions—and yet, from experiments made on other Crustacea, we have every reason for believing that it is this part alone which is capable of digesting and absorbing nourishment. Hence it comes about that the nourishment must be supplied to it in the form of the finest powder, and so a Crustacean—and the same is true more or less of all Arthropoda—is quite incapable of either swallowing its prey whole or even of bolting large morsels of food.

From the mouth the so-called oesophagus ascends upwards and slightly forwards till it expands into the so-called stomach, which is divided by a deep transverse indentation into an anterior "cardiac" portion and a posterior "pyloric" portion, these names being suggested by fanciful analogies with parts of the human stomach. Both oesophagus and stomach are simply portions of the stomodaeum and of course like the rest of the ectoderm are covered with cuticle internally. In the case of the stomach this cuticle is thickened in places so as to form firm sclerites some of which have tooth-like projections which are brought together by the action of muscles attached to the stomach and so constitute a mill by means of which the food which has already been torn into fragments by the gnathites is ground up into a powder. This powder is sifted through a sieve of setae which guard the entrance to the pyloric sac; in this way only the finest grains reach the short portion of the intestine lined by endoderm. The muscles which cause the grinding action of the stomach are two pairs, termed the anterior gastric and posterior gastric respectively. These are longitudinal bands arising from the skin under the carapace and inserted in the sclerites in the stomach wall. The anterior gastric muscles arise from the anterior part of the carapace and are attached to a transverse sclerite in the upper wall of the cardiac portion of the stomach termed the cardiac ossicle, whilst the posterior gastric muscles arise from the posterior part of the carapace and are attached to a sclerite called the pyloric ossicle which runs transversely in the upper wall of the pyloric portion of the stomach. The action of these muscles is to drag asunder the cardiac and pyloric ossicles and to stretch the wall of the stomach between them. When the muscles relax the elasticity of the lining of the stomach restores it to its former shape. With each end of the cardiac ossicle there articulates a sclerite called the pterocardiac ossicle which curves downwards and backwards along the side of the stomach, and similarly with each end of the pyloric ossicle a zygocardiac ossicle articulates which curves

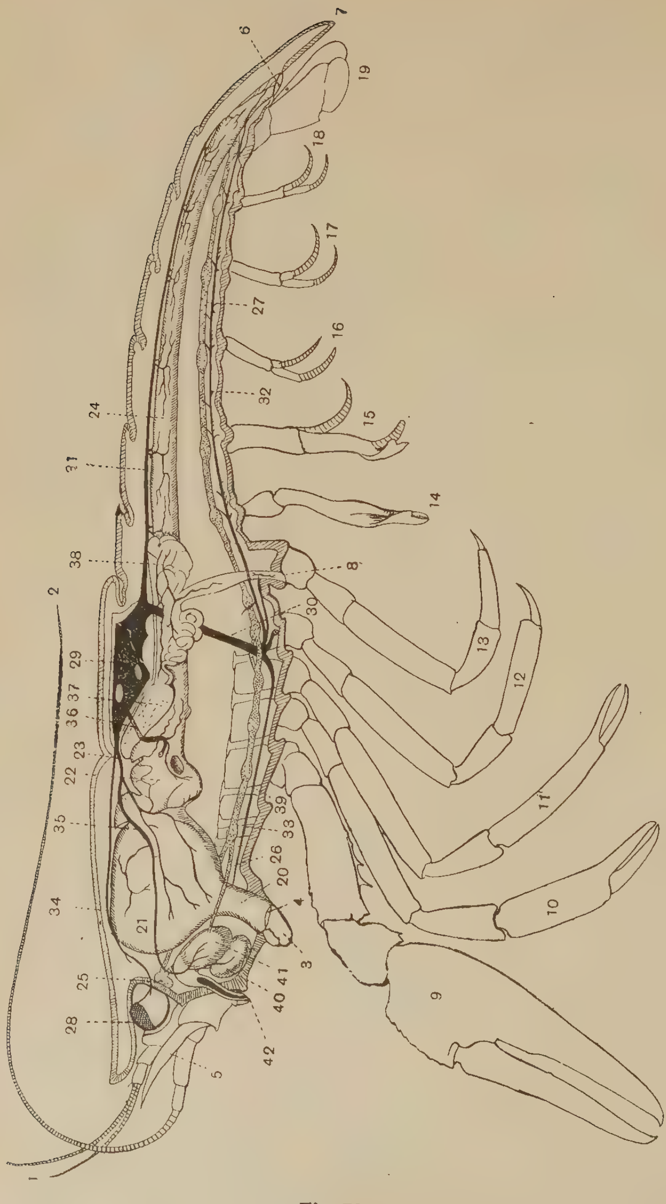


Fig. 73.

FIG. 73. The Crayfish, *Astacus fluviatilis*, split into two by a median cut extending along the mid-dorsal line and viewed from the side.

1. Antennule. 2. Antenna. 3. Mandible. 4. Mouth. 5. Squame of antenna. 6. Anus. 7. Telson. 8. Male genital opening. 9. Chela. 10. First walking leg. 11. Second walking leg. 12. Third walking leg. 13. Fourth walking leg. 14. The first abdominal appendages modified for copulation. 15. The second abdominal appendages also modified for copulation. 16. The first swimmeret. 17. The second swimmeret. 18. The third swimmeret. 19. The tail fan—last abdominal appendage. 20. Oesophagus. 21. "Stomach." 22. Mesenteron. 23. Cervical groove. 24. Intestine. 25. Cerebral ganglion. 26. Nerve-collar. 27. Ventral nerve-cord. 28. Eye. 29. Heart. 30. Sternal artery (ventral part). 31. Abdominal artery. 32, 33. Sternal artery (sub-neural part). 34. Ophthalmic artery. 35. Antennary artery. 36. Hepatic artery. 37. Testes. 38. Vas deferens. 39. Apodemes. 40. Kidney (glandular part). 41. Kidney (bladder). 42. Kidney (opening).

downwards and forwards on the lateral wall of the stomach to meet and articulate with the pterocardiac ossicle. The lower end of the zygocardiac ossicle is produced inwards into a comb-like lateral tooth. The cardiac, pyloric, pterocardiac and zygocardiac ossicles form a hexagonal frame of rods jointed together; so that when the two ends are pulled apart the sides come inwards and the lateral teeth meet and collide. But this is not all; to the centre of the cardiac ossicle is articulated a median sclerite, the urocardiac, running directly backwards, and to the centre of the pyloric is articulated a similar sclerite, the prepyloric, running downwards into the groove dividing the urocardiac and pyloric divisions of the stomach till it meets the urocardiac ossicle. Articulating with both is the median tooth, a sclerite projecting into the stomach. When the cardiac and pyloric sclerites are dragged apart the urocardiac ossicle draws the median tooth forward whilst the end of the prepyloric ossicle rotates it upwards and turns the biting surface of the tooth forward and it comes into contact with the lateral teeth. By the action therefore of the gastric muscles the three teeth are caused to collide. The whole arrangement is termed the gastric mill.

The portion of the intestine lined by endoderm is termed the mesenteron and it is not more than $\frac{1}{8}$ inch long: it is produced dorsally into a slight pouch called the caecum, whilst at each side it is joined by the duct of a large gland called the liver. This organ might be described as a pair of trees of tubes: it consists on each side of a branched outgrowth of the mesenteron—the cells lining which are impregnated with pigment and produce a juice which has a powerful digestive action on the food. It

thus corresponds in function to the pancreas of the Vertebrata rather than to the liver (see p. 429). What cannot be digested passes out by the perfectly straight intestine which is simply the proctodaeum and is of course lined by cuticle. The alimentary canal is surrounded by a series of spaces which used to be regarded as equivalent to the coelom of the Annelida. This however is not a correct view of their nature. The spaces in question are simply blood spaces. From the study of the development of the simplest known Arthropod, *Peripatus*, it is concluded that the coelomic cavities, which in the embryo are just as well represented as they are in Annelida—dwindle in size as growth advances and are represented finally merely by the cavities of the kidneys and of the generative organs, whilst the blood spaces enlarge and take on the character of a body-cavity which is then termed a haemocoele in order to distinguish it from the true coelom. In *Peripatus* there is corresponding to each segment a pair of coelomiducts, the so-called "nephridia" which open internally into minute thin-walled sacs, the remnants of the coelomic sacs. In the crayfish however there is but one pair of greatly enlarged "nephridia" which open in front of the mouth by pores situated as already described on the coxopodites of the second antennae. Each of these kidneys consists of an oval thin-walled sac, developed by an intucking of ectoderm, termed the ureter, in which the excretion accumulates, and by the muscular contraction of which it is expelled, and of a greenish glandular mass situated beneath the ureter, which is the secreting portion of the kidney. This latter portion consists of a network of tubes opening into one another, connected on the one hand with the ureter and on the other with a small thin-walled sac—the end sac—which is the last trace of the coelomic cavity belonging to this segment. The tubes are lined with excretory cells and since the whole organ is bathed in blood the network arrangement of the tubes permits of the exposure of a large surface to the surrounding fluid from which the excreta are attracted by the excretory cells.

It must however excite no small surprise that an active and muscular animal like the crayfish should be able to accomplish its excretion by means of a single pair of excretory organs whilst sluggish animals like the Annelida and even *Peripatus* require a pair of such organs in each segment.

We are forced to the conclusion that some other organ must assist the "nephridia" in carrying out their function, for there is no question that the active metabolism of the crayfish must produce

more waste than that of the worm. Some experiments which Dr Eisig of Naples made on the Capitellidae, a family of Polychaeta, seem to throw light on this subject. When he injected into these animals a coloured poison like indigo-carmine, a large part was excreted by the nephridia, the cells of which became deeply coloured with the material they extracted from the coelomic fluid. Part was however got rid of by the skin, and was thrown off mixed with the substance of the cuticle and was even incorporated with the chaetae. From these facts Dr Eisig concluded that a portion of the waste products of metabolism was eliminated through the skin. Now in the crayfish the ectoderm consists of a single layer of pillar-shaped cells, which are continually secreting at their outer ends the material called chitin which contains nitrogen and is stated by some authorities to be chemically allied to guanin and uric acid, substances which are in many animals produced by the kidneys. As this secretion goes on the shell increases in thickness, and confines the growth of the animal. So at intervals this hard casing of dead matter is thrown off: the old shell cracks along the mid-dorsal line, and the animal gradually extricates itself, and the cuticular lining of the stomodaeum and proctodaeum is cast at the same time (Fig. 74). The whole process is called ecdysis, and it occurs five or six times in the first year, twice in the second year and after that once a year. After each ecdysis the skin remains soft and growth can take place, but of course during this period as the animal is defenceless it remains hidden. Thus the tendency of the ectoderm to produce chitin has not only governed the form which the locomotor and masticatory organs have assumed but it has had the indirect effect of causing the coelom and nearly all the excretory organs to disappear, since the skin has assumed most of the excretory functions.

The genital organs have the same shape and position in both males and females: they are situated beneath the pericardial septum which is a sheet of connective tissue forming the floor of the pericardium. In each sex the organ has a trilobed shape; there are a pair of anterior lobes and a single median posterior lobe. It is hollow and is connected with the exterior by a pair of ducts which spring from the sides just where the paired anterior lobes pass into the posterior one, and open to the exterior by a pair of pores situated in the male on the coxopodite of the last pair of thoracic legs, but in the female on the coxopodites of the third pair (in each case counting the chela as the first leg). From the cells lining the cavity of the gonad are produced the ova, which are about the size

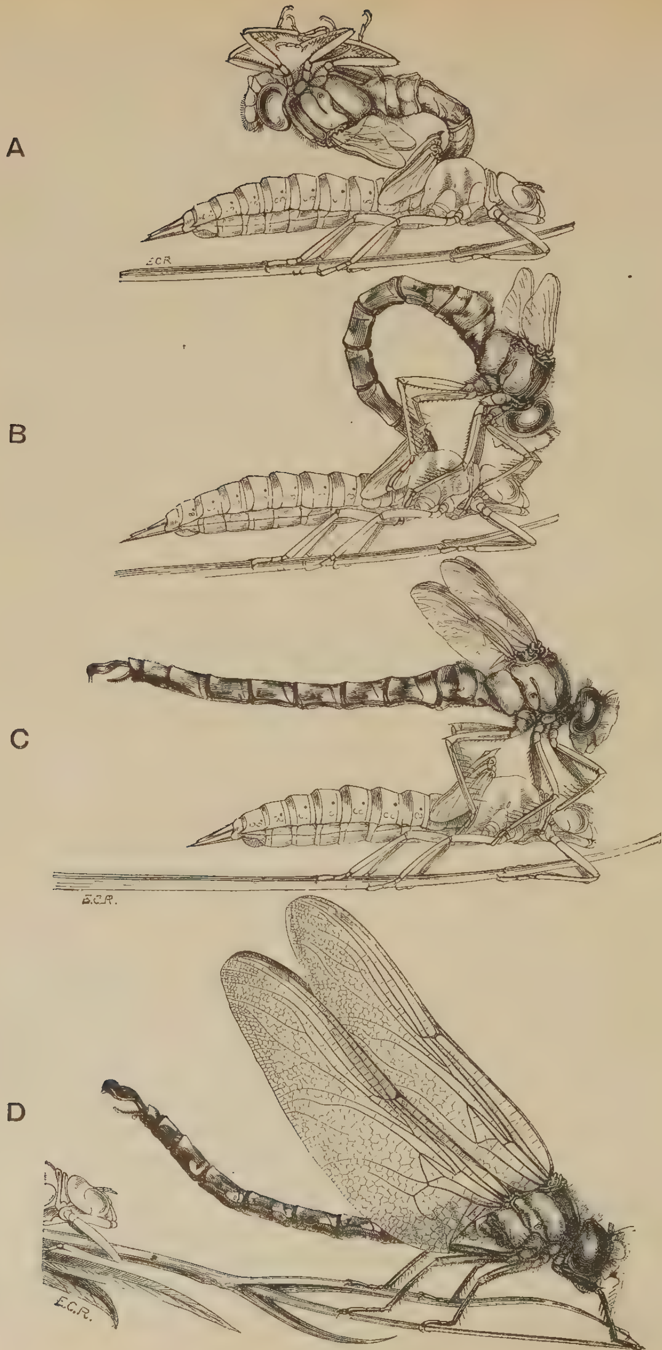


Fig. 74.

FIG. 74. To illustrate the process of "ecdysis" in Arthropoda.
A. The anterior portion of the body of a Dragon-fly, *Aeschna cyanea*, freed from the larval shell. B. The tail being extricated. C. The whole body extricated. D. The perfect insect, the wings having acquired their full dimensions, resting to dry itself preparatory to the wings being horizontally extended.

of pellets of shot and are filled with a dark red yolk. These when ripe are shed to the exterior through the short straight oviduct and become attached to the swimmerets of the abdomen by their adhesive coats, and in this position they are fertilised and accomplish their development, becoming free from the mother only when they have become little crayfish.

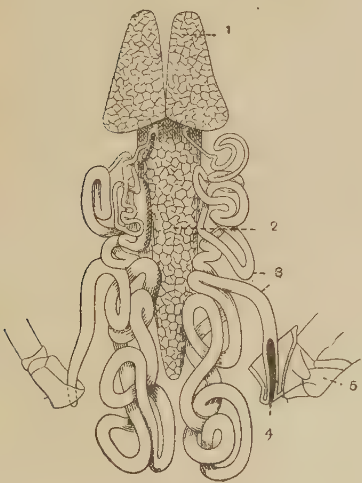


FIG. 75.

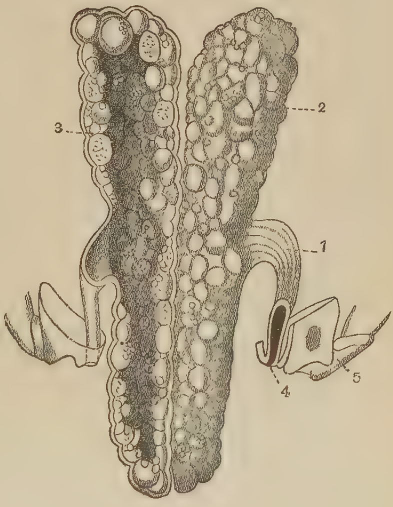


FIG. 76.

FIG. 75. Male reproductive organs of *Astacus fluviatilis* × about 2½. From Howes. 1. Right anterior lobe of testis. 2. Median posterior lobe of testis. 3. Vas deferens. 4. External opening of vas deferens. 5. Right fourth ambulatory leg in which the vas deferens opens.

FIG. 76. Female reproductive organs of *Astacus fluviatilis* × about 2. From Howes. 1. Right oviduct. The left oviduct is shown partly opened. 2. Right lobe of ovary. 3. Left lobe of ovary with the upper half removed to show the cavity of ovary or coelom into which the ripe ova drop. 4. External opening of oviduct. 5. Right second ambulatory leg on which the oviduct opens.

From the lining of the testes male germ-cells are formed—we say advisedly, male germ-cells—not spermatozoa, for these cells are utterly unlike spermatozoa. They are rounded saucer-shaped cells with a central nucleus and a number of curved spines sticking out tangentially from the surface by means of which they adhere to the

ova. The nucleus is in the centre at the bottom of a chitinous tube which seems capable of being turned inside out and thus forcing the nucleus into the ovum. The male duct or vas deferens is long and coiled, and for part of its length is lined by cells which produce a milky fluid in which the male cells float. When this fluid with its contained cells escapes from the male pore it is received by the tube formed by the two first pairs of appendages of the abdomen, and the male then seeks the female and turning her on her back, discharges the fluid on to the eggs.

Nothing could more strongly illustrate the proclivity which the protoplasm of the Arthropoda has towards the production of cuticle than the substitution of these motionless male cells with their spiny covering for the active motile spermatozoa. One cannot but believe that spermatozoa would be more advantageous, especially for aquatic animals, and other groups of the Arthropoda such as the Arachnida, have managed to retain them, but in these Crustacea the set towards the production of cuticle appears to be so strong that they have become an impossibility. The study of the development of *Peripatus* teaches us, that not only are the genital organs of Arthropoda remnants of coelomic sacs but that the genital ducts are the remnants of the coelomiducts or "nephridia" opening into these sacs. Therefore, in the crayfish there are three pairs of "nephridia" left; one pair acting as kidneys, one as oviducts, one as vasa deferentia.

The nervous system of the crayfish is constructed on the same type as that of the Annelida, differing in details only, though these details are most instructive. It consists of a brain, situated in front of the mouth, communicating by means of a nerve-collar, which encircles the oesophagus, with a ventral chain of ganglia. The differences are as follows. In the Annelida the nuclei of the neurons are scattered all along the ventral cord, being only less numerous in the commissures than in the ganglia. In the Crustacea, and indeed all Arthropoda except *Peripatus*, the nuclei are confined to the ganglia and the commissures consist of axons (nerve-fibres) only. Further, in most Annelida the cord is apparently a single one, though the microscope shows that it consists of a double strand of fibres—but in the crayfish it is clearly a double one in thorax and apparently a single one in the abdomen.

Finally the ganglia of several adjacent segments show in some cases a tendency to coalesce so that there are considerably fewer ganglia than segments as indicated by the appendages. Thus the brain supplies nerves not only to the eye region which we may suppose to represent the prostomium of Annelida but also to the

two pairs of antennae which were originally pairs of appendages situated behind the mouth, whilst the first ganglion of the ventral chain termed the sub-oesophageal sends nerves to all the primary jaws and to the first two pairs of maxillipedes, so that it represents five ganglia fused together. The ganglion which supplies the third maxillipede is separated from the sub-oesophageal ganglion only by a groove, and Huxley considered it a part of the sub-oesophageal, which on this reckoning would supply all the jaws. Each of the "legs" and of the swimmerets is supplied by a separate ganglion, though the ganglia for the fourth and fifth legs are very close together. The commissures between the ganglia for the third and fourth leg diverge widely to allow the sternal artery to pass between them.

In higher Crustacea such as the Crabs the coalescence of the ganglia has gone much further so that all the jaws and all the thoracic appendages are supplied by a single ganglion.

The principal sense organs of the crayfish are the eye and the ear. The eye is a modification of the ectoderm covering the tips of the eye-stalks. It consists fundamentally of a number of pits of ectoderm each of which becomes filled with the secretion of the cells forming its walls. It is termed a compound eye to distinguish it from the eyes found in other Arthropoda which consist of a single pit of ectoderm. Starting from the surface each pit consists of a pair of lens cells which secrete ordinary cuticle rather more vigorously than the surrounding ectoderm. Hence a slight convexity of the cuticle is occasioned which acts as a plano-convex lens to concentrate light on the pit. Below the lens cells is a circle of four cells, each of which secretes on its inner side a mass of clear material—the conjoined secretions of the four cells constitute a clear body termed the crystalline cone. Below these again come a circle of six or seven visual sense cells, each of which develops the characteristic visual rod on its inner side whilst from its basal end a nerve fibre proceeds inwards. The visual rods all coalesce to form a fluted striated spindle called the rhabdome and the group of visual cells is termed the retinula.

Each eye-pit is surrounded by dense black pigment contained in amoebocytes which wander into this position from the surrounding blood. As a result of this investment of pigment the only light which can penetrate the pit and affect the retinula consists of rays very nearly parallel to the axis of the pit. All slanting and oblique light will be absorbed by the pigment layer, and so the retinula is

stimulated by the colour and intensity of the light proceeding from a small area of the outside world directly in front of it. Since the eye consists of a great number of pits, it follows that an image is formed as a mosaic or pattern of light and shade, depending on the extent to which each individual retinula is stimulated. The fineness and exactness of the image will depend on the number of eye-pits and retinulae. The principle of the formation of this image is exactly similar to that on which the image is formed in the human eye—viz. the concentration of the light from a particular area of the outside world on a particular element of the eye, only that the form of the human lens enables a much larger beam of light to be concentrated on each element, and the number of elements is large, so that the image in the crayfish's eye is dimmer and coarser than the image in our own. The sensations from all the various eye-pits are transmitted by the basal fibres of the retinula cells to the optic ganglion situated in the centre of the eye-stalk, by which they are combined and the resultant image is transmitted to the brain.

The optic ganglion is developed by a budding of the ectoderm cells along the side of the stalk. In shrimps, as already mentioned, when this ganglion is destroyed an antenna-like organ is developed in place of the eye, but if it remains intact the stump of the eye-stalk will produce a new eye.

The ear is a very much simpler organ than the eye. It is merely an open ectodermic pit, lined with cuticle, situated on the upper surface of the basal segment of the antennule. The entrance is guarded by rows of feather-like setae which extend from the side across the opening. Over the bottom of the pit are several parallel rows of delicate simple setae, the bases of which are in close association with sense cells, and the nerve fibrils proceeding from these cells form the auditory nerve, which goes to the brain. These delicate setae it may easily be imagined will respond to vibrations traversing the water: and the information thus conveyed to the animal may warn it against the approach of its enemies, though these vibrations would not be perceptible to our ears as sound. But experiments have shown that as is the case with so many ears, another and different function is carried out by the organ to which the perception of vibrations may be quite subsidiary, viz. the perception of the position of the animal with regard to the vertical—or the perception of balance. These experiments were carried out on the sea crayfish *Palinurus*. The ear-pit contains

particles of grit or sand which will roll into different positions and stimulate different sense-cells for each new position which the animal assumes. When however the animal undergoes ecdysis the cuticle lining the ear-pit is shed and with it these grains of grit. After each ecdysis therefore the animal must obtain fresh grains of sand from outside. Now the experimenter kept specimens of *Palinurus* in a tank till they shed their shells which he immediately removed. The animals were then placed in filtered sea-water to which some grains of magnetic oxide of iron were added. In a day or two when the new shell had hardened and the crayfish regained their activity the experimenter approached the tank with a powerful magnet. The animals then set themselves at right angles to the lines of magnetic force; they behaved as if the magnetic attraction were the force of gravity. This could only be explained on the assumption that they regulated the positions of their bodies in accordance with the position of the particles of grit in the ears—in other words the balancing function of the ear was proved.

The sense of smell is also situated in the antennule and is no doubt one of the most important senses the animal has, but the only organs which can be associated with it are the small flattened setae on the exopodite already described. The sense of touch is probably associated with the small setae scattered all over the body. Each of these is inserted by means of a tiny arthrodial membrane in the shell and is consequently moveable, and sense cells are situated at the bases of many of them which must be stimulated when anything moves these tiny levers.

The muscles of the crayfish practically all consist of bundles of longitudinal fibres which must be regarded as remnants of the walls of the vanished coelomic sacs. There are no circular muscles, except those surrounding heart and arteries, for the comparatively rigid shell in which the animal is enclosed would make circular muscles useless. The muscles may be divided into trunk muscles and appendage muscles, and we may treat of the latter first. The skeleton of each segment of each appendage articulates with each succeeding and preceding segment, so that it can move with respect to each of them in only one plane. To effect this movement two muscles are necessary, an extensor, or straightener, and a flexor, or bender. Since the skeleton is outside the muscles, the flexor muscle is placed on the opposite side of the limb from that towards which it is bent, the reverse of the condition which prevails in the

human limb where the skeleton is internal. In each segment of each limb (except the most distal) there are four muscles, two flexors and two extensors connecting it with its predecessor and successor, but the plane in which any one segment can move on its successor is different from that in which it moves on its predecessor; in fact, there is a different plane of movement between every pair of segments, so that by the combined movement of every joint the limb can be bent into any position. [The construction of the crayfish's limb has been imitated by a firm of American instrument makers who have produced a lens-holder on this plan which can be bent into any shape.] The muscles which move the mandibles are very powerful, the adductor which brings them together forming a great fleshy mass at the side of the stomach. Each abdominal segment is connected with the next by a pair of flexors and extensors, and since the downstroke is, as we have seen, the motion by which the crayfish swims backwards the flexors form a very much thicker bed of flesh than do the extensors. The intestine lies above the flexors and below the extensors. From the first segment of the abdomen extensors and flexors pass into the thorax, in each case breaking up into several slips of muscle which are inserted in different segments of the thorax, indicating that the segments of the thorax, though now immovably fused with one another, were once movable. The cells of which the muscles are composed are very different from the muscle-cells described in the Annelida. Muscle-cells of that description are, it is true, found in the muscular walls of the heart and arteries and intestine of the crayfish, but the muscles by which the quick movements of the body-segments and appendages are carried out are composed of muscle-cells of a more complex kind. These are much longer than the spindle-shaped muscle-cells of *Lumbricus*, and are clothed with a delicate cuticle called the sarcolemma; they each have numerous nuclei which are embedded in unmodified protoplasm, and the remainder of the protoplasm is converted into contractile fibrils. These fibrils are of a composite nature, being made up of alternate discs of a lighter, apparently semi-fluid, material and a darker solid doubly-refracting material. Each fibril is divided into a series of segments or sarcostyles, each sarcostyle consists of a disc of doubly refracting or anisotropic substance with a disc of singly refracting isotropic substance on each side. Each sarcostyle is separated from the next by a thin membrane, "Krause's membrane." When contraction occurs the isotropic substance is absorbed by the anisotropic which swells and

at the same time becomes lighter in colour. Such muscles are able to carry out much more rapid contractions than is the case with the unstriped smooth muscles, and as they recover from the state of contraction with great rapidity many quickly succeeding contractions can be carried out. In the case of the Mosquito, which produces its note by the vibration of the wings, it has been calculated that at least 5000 contractions a second must be effected by the wing-muscles. Speaking broadly, muscles of this type are found only in Arthropoda and Vertebrata, but they occur in other groups of the animal kingdom in the case of isolated muscles (cf. jaw-muscles of Echinoidea), where rapid and powerful movements are required.

The muscles are inserted in the skin, but in the thorax this is folded inwards between the segments so as to produce wedges termed apodemes which project into the body cavity and give attachment to the flexor muscles. The apodemes are, of course, stiffened by a deposit of chitin between the two layers of ectoderm of which they are composed. Between all the segments which bear the "legs," except the last, two apodemes project inwards on each side, one arising from the side, called the endopleurite, and one from the ventral surface, called the endosternite. The two endosternites of opposite sides meet in an arch, enclosing the sternal canal, in which lies the nerve cord. On its outer side the endosternite forks and one fork, termed the arthrodial apodeme (*ap.arth*, Fig. 71), meets a corresponding process of the endopleurite, and the two form a strengthening wall round the insertion of the limb. The endosternite has a third process, termed the paraphragmal (*ap.par*, Fig. 71), which passes forward to unite with the endopleurite in front, so that a somewhat complicated internal skeleton results. At each ecdysis the chitin which stiffens the apodemes is moulted, and at that time the apodemal fold could be straightened out. In some Crustacea, though not in the crayfish, very marked changes in the shape of the animal are brought about at ecdysis by the smoothing out of apodemes, and the development appears to proceed by sudden jerks.

Connective tissue has already been mentioned in the case of the Platyhelminthes, Rotifera and Annelida, but in these animals it attains little development compared with that which it reaches in the case of the Arthropoda. It consists, it will be remembered, of a semifluid ground-substance, corresponding to the jelly of Coelenterata, which becomes invaded by amoebocytes. These by their metabolism

manufacture bundles of white tough fibres which interlace in such a way as to produce a membrane of great strength. A special development of this connective tissue underlies the ectoderm and is termed dermis—it is included along with the ectoderm in the popular term skin. But connective tissue is ubiquitous in the crayfish, if as Huxley said we could imagine the essential cells of every organ dissolved there would remain a cast of the whole in connective tissue.

Blood may be regarded as a tissue of the same kind as connective tissue—only here the ground-substance is thoroughly fluid, the amoebocytes or blood cells not depositing fibres. As already mentioned, in the crayfish all the crevices between the various organs are occupied by blood, these cavities taken together being termed the haemocoele. Of these the largest is the pericardium, a space just under the dorsal wall of the thorax which is divided from the rest by the horizontal pericardial septum—a structure which from observations on the development of other Arthropoda we learn to be derived from the dorsal portions of the coelomic sacs, which have flattened out and lost their cavities. The pericardium communicates with certain vertical canals in the thin side-walls of the thorax (i.e. the true walls, not the branchiostegite), termed branchio-cardiac canals. These canals are in communication with the gills, and through them the blood that has absorbed oxygen there is returned to the pericardium. Each gill has a hollow stem traversed by a longitudinal septum which divides its cavity into two spaces, an upper and a lower, only communicating at the tip. The branchio-cardiac canal communicates solely with the upper passage, whilst the lower communicates with the ventral sinus already mentioned, in which the nerve-cord lies, from which the impure blood passes to the gills.

Returning to the pericardium we find suspended in it by fibrous cords, termed the alae cordis, the heart. This is an oval muscular sac with three pairs of openings, termed ostia (Lat. *ostium*, a door). Each ostium is provided with two flaps which open inwards, but which when the heart is full of blood are pressed together so that they meet and prevent the blood from escaping. Thus the heart receives the blood from the pericardium. When the heart contracts the blood is driven out on all sides through vessels with strong muscular walls called arteries. There are six main arteries—one called the abdominal goes backwards over the intestine, and gives off a branch immediately behind the

heart called the *sternal* artery. This artery goes directly downwards and passing between the commissures connecting the third and fourth pairs of thoracic ganglia divides into anterior and posterior branches which lie beneath the nerve-cord and give blood to it (30, Fig. 73). From the heart an *ophthalmic* artery is given off which runs forwards over the dorsal surface of the stomach and eventually gives branches to the eyes and antennules. In addition there proceed forwards from the heart two pairs of arteries, the antennary and the hepatic. The first pair supply the antennae; each gives off on its way a large branch to the stomach, called the gastric artery. The *hepatic* arteries are more deeply situated, they run forward and break up into branches which are distributed to the tubes of the liver. The muscles surrounding the arteries, as in Vertebrata (see p. 434), do not carry out rhythmical contractions, but keep up a steady pressure on the blood, called *tone*. When the arteries are traced they break up into branches which finally open into the spaces of the haemocoele.

So far no mechanism has been described which drives the blood to the pericardium. It seems to find its way there by the constant pressure from behind of the blood driven out from the heart.

Reviewing the structure of the animal we see that the production of chitin by the ectoderm leads to the jointing of the appendages from which the name Arthropod is derived, leads further to the loss of cilia and the consequent necessity of the peculiar respiratory mechanism, and to the disappearance of the coelom and most of the excretory organs, and consequently to the peculiar form of the genital organs. In fact, it would be hard to name a character of the Arthropoda as distinguished from the Annelida which is not directly or indirectly traceable to the existence of the chitinous shell.

Class I. Crustacea.

The Crustacea are with a few exceptions, such as the Wood-louse, inhabitants of the water, and they breathe either through the general surface of the body or by means of gills. They have or are believed to have once possessed two pairs of antennae and these as well as their other jointed limbs are typically biramous, that is, they consist of a basal portion or protopodite bearing two prolongations, the endopodite and the exopodite. They have at least three pairs of appendages converted into jaws.

The Crustacea are usually divided into two groups, the Entomostraca (Gr. ἔντομος, cut in pieces; ὄστρᾰκον, a shell) and the Malacostraca (Gr. μᾰλᾰκός, supple); and each of these again is divided into four and three Orders respectively.

Sub-class A. ENTOMOSTRACA.

This group may be regarded as a lumber-room for all Crustacea which are not included in the well-defined division Malacostraca, and the only character which can be attributed to all the members is that of not possessing the marks of Malacostraca.

For the most part they are small Crustacea of simple structure. The number of their segments varies within wide limits; some Ostracoda having only seven pairs of limbs, whilst in *Apus* there are sixty-eight pairs. The dorsal part of their head has, in many cases, grown backwards and downwards like a mantle to form a large hood or shell, termed the carapace, which may cover a large part of the body, and in some cases this becomes divided into two lateral halves hinged together like a mussel's shell; but unlike the carapace of the Malacostraca it does not become fused with the terga of the thorax. In many descriptions of Entomostraca the words "thorax" and "abdomen" are used to describe regions of the body. Such terms are in strictness applicable only to the higher Crustacea, where the trunk is sharply differentiated into two regions distinguished by the character of their appendages. Amongst the Entomostraca however the appendages of the trunk form a uniform series: often it is true the last segments are devoid of appendages, and to these the term abdomen (16, Fig. 77) is usually applied, but to us this seems an unjustifiable and misleading use of a term which has an exact significance only amongst Malacostraca.

Entomostraca have no internal teeth in their stomach. As a rule the young are not like their parents but are larvae of a special kind called Nauplii; these after a number of ecdyses, during which the number of segments increases, grow up into adults.

The Nauplius possesses an oval, unsegmented body, a median simple eye, three pairs of appendages and a large upper lip. The first pair of limbs representing the first antennae of the adult are simple and unjointed, the other two pairs have a basal piece and two branches. The inner branch of one or both pairs has a hook for masticatory purposes. These two pairs of appendages become

the second antennae and mandibles of the adult; both are at first placed behind the mouth.

The Entomostraca consists of the following Orders:

Order I. Phyllopoda.

As the name implies the Phyllopoda (Gr. φύλλον, a leaf; πούς, a foot) are characterised by possessing flattened leaf-like swimming limbs. Of these there are at least four pairs but there may be many more. The larger Phyllopoda are not uncommon in Britain; one genus, *Artemia*, taken at Lymington, flourishes in salt-pans in which the salt is so concentrated as to be fatal to other animals. It can be reared by making solutions in distilled water of the substance sold as "Tidman's sea-salt" of 8 °/₀ strength. If a number of such solutions be made, the larvae of *Artemia* will appear in some of them. These larvae can be fed by making decoctions of fresh green leaves in water. They will if carefully tended grow to maturity. *Artemia* is devoid of the carapace and has an elongated heart extending throughout the body. *Branchipus* (Fig. 77) an allied genus occurs in stagnant water, and has been recorded in several localities in the south of England. It is often found in the vicinity of Montreal, in Canada, in the pools of rain water which have accumulated in disused quarries. *Apus* is another of the larger forms which was formerly found in Britain but has not been met with for some years and is possibly now extinct in this country. It has a large carapace, and its flattened leaf-like appendages are regarded as primitive types of the Crustacean limb from which all the numerous modifications of the higher forms may be derived. Of these, eleven pairs are situated in front of the genital opening and often termed "thoracic," one pair being attached to each of the pre-genital segments of the trunk. Behind the genital opening there are fifty-two so-called "abdominal" pairs of legs, of which several pairs are attached to each post-genital segment except the last two or three.

The genera *Simocephalus* and *Daphnia*, common in ponds and ditches, both in England and America, differ from the foregoing in having fewer segments and in possessing a bivalve carapace which completely encloses the body. The first antennae, or, as they are generally called, the antennules, are small and simple,

but the second antennae are very large and forked and project from the shell, and by their lashing movement carry the animal through the water (Figs. 78 and 79). The carapace is to a certain extent transparent, and through it the beating of the heart, the circulation of the blood and the movements of the thoracic leaf-like appendages may be made out. Within the substance of each valve of the carapace a coiled glandular tube may be detected; this is the **shell-gland** or typical excretory organ of the Entomostraca which opens to the exterior in the region of the second maxilla. The male (Fig. 78) is usually smaller than the female (Fig. 79), and is certainly very much rarer. The females lay two kinds of eggs, (i) unfertilised eggs, which develop in the space intervening between the dorsal side of the body and the shell which acts as a brood-pouch, and (ii) fertilised eggs, which are larger and become surrounded by a special modification of the brood-pouch called the **ephippium**. The nature of the eggs produced is regulated by favourable or unfavourable conditions of life. At a suitable temperature and with a sufficiency of food and water, the unfertilised eggs are produced in large numbers at short intervals. Periods of drought or the cold of winter bring about the formation of eggs which are fertilised and enclosed in the ephippium. Sheltered by this case the eggs are enabled to withstand freezing or desiccation and with a return of suitable conditions a young *Daphnia* hatches out from each egg to continue the cycle of life.

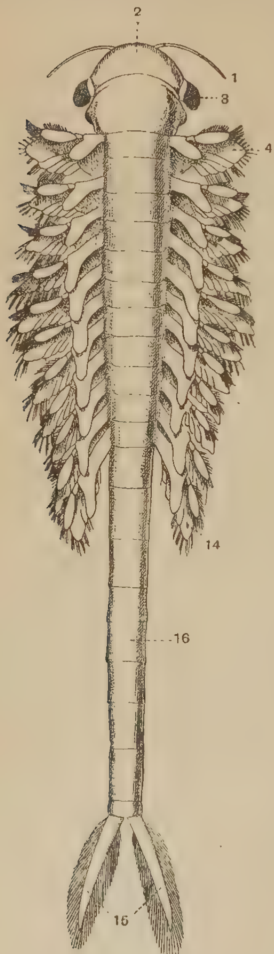


FIG. 77. Dorsal view of female, *Branchipus* sp. found in a pond in Sussex × about 10.
1. Antennae. 2. Head. 3. Eyes. 4—14. The eleven "thoracic" limbs. 15. The caudal forks. 16. The fifth "abdominal" segment.

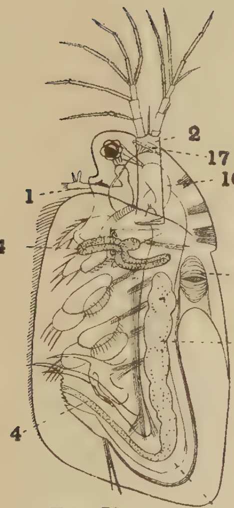


FIG. 78.

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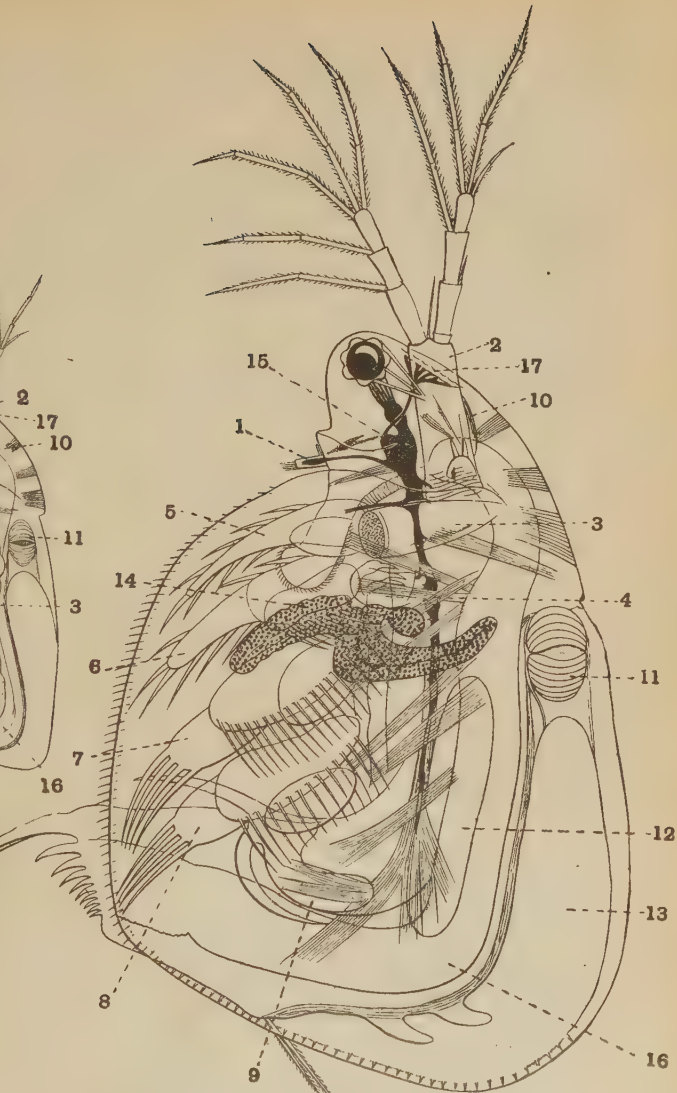

FIG. 79.

FIG. 78. Side view of male *Simocephalus sima*. Highly magnified. 1. Antennules. 2. Antennae. 3. Testis. 4. Vas deferens. 10. Hepatic diverticulum. 11. Heart. 14. Shell-gland. 16. Mid-gut. 17. Neck organ.

FIG. 79. Side view of female *Simocephalus sima*, magnified to the same extent as Fig. 78. From Cunnington. 1. Antennules. 2. Antennae. 3. Mandibles. 4. Maxillae. 5. 1st pair of legs. 6. 2nd pair of legs. 7. 3rd pair of legs. 8. 4th pair of legs. 9. 5th pair of legs. 10. Hepatic diverticulum. 11. Heart. 12. Ovary. 13. Brood-pouch. 14. Shell-gland. 15. Brain. 16. Mid-gut. 17. Neck organ.

The Phyllopoda are divided by Dr Calman, our best authority, into four sub-orders, viz.:

Sub-order 1. **Anostraca.**

Long-bodied Phyllopoda devoid of a brood-pouch and of carapace, the second antennae are not used as swimming organs but are converted into curious claspers by which the male grasps the female. Ex. *Artemia*, *Branchipus*.

Sub-order 2. **Notostraca.**

Long-bodied Phyllopoda with a broad flattened carapace. Antennules and antennae vestigial. Ex. *Apus*.

Sub-order 3. **Conchostraca.**

Phyllopoda with a bivalve carapace. Body of moderate length, antennae forked and used for swimming.

Sub-order 4. **Cladocera.**

Phyllopoda similar to the Conchostraca but with still shorter bodies using the space between carapace and body as a brood-pouch. Ex. *Simocephalus*, *Daphnia*.

The Anostraca, Notostraca, and Conchostraca live in fresh water and as a rule in the standing water of pools and ponds; they are more rarely found in brackish or salt water. They swim actively about by means of the vibrations of their flattened limbs. As a rule aquatic animals swim with the upper surface towards the surface of the water, but the Phyllopoda seem very indifferent to this rule, and are quite frequently seen swimming upside down. The Cladocera almost always swim upside down, the genus *Daphnia* however usually adopts a vertical position with the head uppermost. These last are much the most widely distributed group of the Phyllopoda. There are not only fresh-water but also many marine species. The latter occur in great swarms in many parts of the ocean.

Order II. **Ostracoda.**

This order (Gr. ὀστρακώδης, shell-like) contains a great number of species which do not differ greatly from one another in outward appearance. In form they resemble *Daphnia*, but the head does not protrude from between the valves of the carapace, and some of the internal organs of the body, viz., the ovary or testis and branches of the liver, are prolonged into the valves of the carapace. This latter is a very characteristic structure, consisting, like the shell of the

Mussel, of two valves. It opens by an elastic ligament which tends to pull the valves apart, and it closes by the contraction of a muscle which runs across the body from one valve to another. The whole body is included in the carapace, antennae and all.

Ostracoda have fewer appendages than any other group of Crustacea; besides the antennules, antennae, mandibles and two pairs of maxillae, they possess only two pairs of limbs, and these are stout and cylindrical in marked contrast to the appendages of the Phyllopoda. The hinder part of the body is rudimentary.

Two pairs of excretory organs have been described in some species of Ostracoda, the shell-glands common to all Entomostraca opening at the base of the second maxillae and a pair of antennary glands opening at the base of the second antennae. The last named are seldom found except in the Malacostraca.

Both pairs of antennae are used in swimming, another most important distinction from *Daphnia* and its allies.

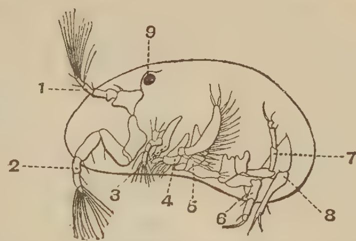

Fig. 80. Lateral view of *Cypris candida*. After Zenker.

1. Antennules. 2. Antennae. 3. Mandibles. 4. 1st maxillae. 5. 2nd maxillae. 6. 1st pair of legs. 7. 2nd pair of legs. 8. Tail. 9. Eye.

The males differ from the females, which either (*Cypris*) lay their eggs on water-plants or (*Cypridina*) carry them about within their shells. The majority of species are found in the sea but others occur in fresh water. They are flesh eaters, and as they exist in great numbers they fulfil the important duty of scavenging on a small scale, and thus they prevent the accumulation of dead organic matter in the water. They are divided into two main divisions: (*A*) Podocopa with unbranched second antennae, inhabitants of shallow shore waters which do not swim strongly but creep a good deal. (*B*) Myodocopa with powerful forked second antennae and a notch in the edge of each valve of the carapace to allow the antennae to be vigorously moved; they are inhabitants of deeper waters. Fossil Ostracoda are found in the oldest fossiliferous rocks.

Order III. **Copepoda.**

This order Gr. κώπη, oar; πούς, ποδός, foot) is also a large one and its free-swimming members exhibit a very characteristic structure and

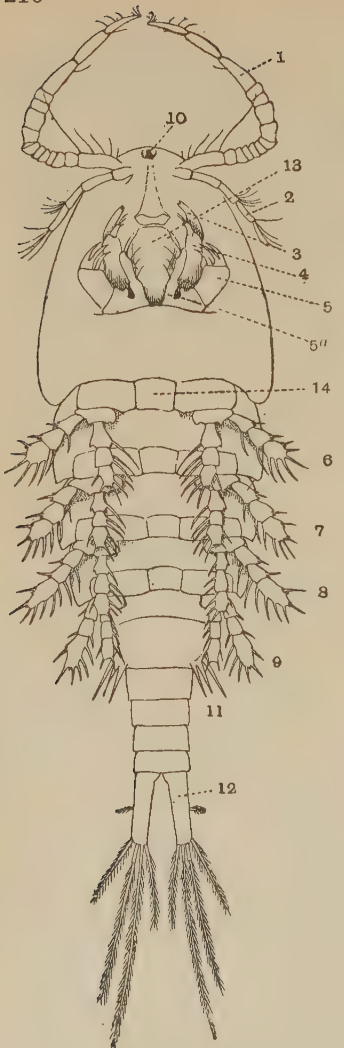

FIG. 81. Ventral view of male *Cyclops* sp. Magnified.

1. Antennule. 2. Antenna. 3. Mandible. 4. 1st maxilla. 5. The two halves of the 2nd maxillae sometimes called inner and outer maxillipedes. 6–9. 1st–4th thoracic limbs. 10. Eye. 11. Bristles near male generative opening. 12. Caudal fork. 13. Mouth. 14. Copula or plate connecting the right and left limb of each pair.

appearance. The body is of an elongated pear shape, and consists of a large round head and a tapering trunk of comparatively few segments. The carapace so characteristic of the preceding order is entirely absent. The head bears a single median eye in front, the lateral compound eyes so conspicuous in most Crustacea being absent. Attached to the head are six pairs of appendages, two pairs of antennae, a pair of mandibles, two pairs of maxillae and a pair of short but jointed leg-like appendages termed maxillipedes. The head is not separated from the trunk by any constriction. The latter bears four pairs of swimming feet of a typical forked pattern. Each of these appendages is something like a λ. The base of the limb consists of one or two joints constituting the protopodite. The two forks are of course the exopodite and endopodite. Both are flattened, consisting of stout joints each of which bears spines, and the whole forms a convenient paddle. Each limb is also jointed to its fellow of the opposite side by a transverse movable ridge so that the right cannot move without the left. By the simultaneous action of all the limbs of the trunk, the animal is enabled to execute a series of swift darts through the water; by the action of the second antennae a slow, gliding movement is carried out, whilst the maxillipedes by sweeping movements

search the water for food. A forked limb, as we have seen, is characteristic of the Crustacea, and is not met with in other groups of the Arthropoda. It appears over and over again in all the orders,

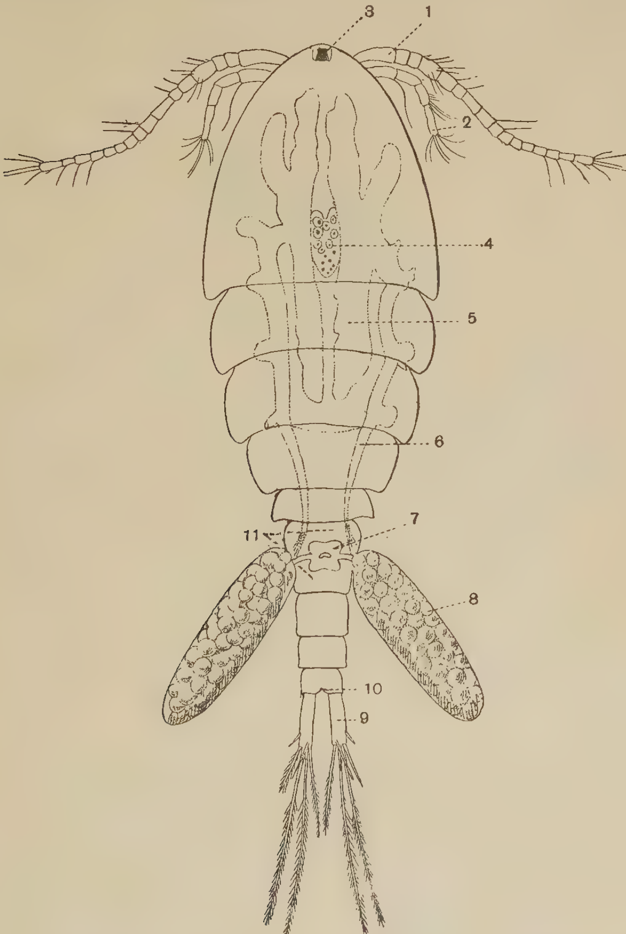

FIG. 82. Dorsal view of female *Cyclops* sp. Magnified. Partly after Hartog.

1. 1st Antenna. 2. 2nd Antenna. 3. Eye. 4. Ovary. 5. Uterus, i.e. pouch of the oviduct into which the eggs pass before being shed. 6. Oviduct. 7. Spermatheca or pouch for receiving the spermatozoa of the male. 8. Egg-sacs. 9. Caudal fork. 10. Position of anus. 11. Compound segment, consisting of the last thoracic (bearing the genital opening) and the first abdominal.

retaining its primitive form in some instances, as in the abdominal appendages of a Crayfish; but more often, by the suppression of one

part (usually the exopodite) and by the development and modification of others, the original form becomes masked and difficult to recognise. When both forks are conspicuously developed the limb is said to be biramous. The last four or five segments of the Copepod's body bear no appendages. The last is produced into two processes, forming a caudal- or tail-fork.

The sexes in the free-living species are not markedly different, but if we examine specimens of such a genus as *Cyclops*, which is common in our fresh-water pools, we shall find that in the breeding season the female carries about with her two egg-sacs (Fig. 82). These are attached to her body just behind the last pair of appendages and project freely at the side. Each egg-sac may contain four or five dozen eggs which are glued together by a cement-substance. Such egg-sacs are very characteristic of the Copepoda and are found even in the parasitic members of the order. Most of the latter live on fish, and some have acquired the name of "fish-lice." Their mouth appendages have lost their biting function and have become adapted for piercing the tissues of the host on which they live. Their segmentation is suppressed and their appendages are reduced and the body has grown out into all sorts of curious processes. The male is often much smaller than the female and as a rule retains the crustacean characters more than she does. Occasionally they are found on the skin of a fish, but more often they occur in the mouth and on the gills, sometimes half and sometimes wholly embedded in the flesh of their host.

Order IV. **Cirripedia.**

Some of the Copepods have become so modified by their parasitic habits that unless we were able to trace their development, including the larval forms through which they pass before becoming adult, we should have difficulty in assigning them to their proper place amongst the Crustacea. A somewhat similar modification occurs in the Cirripedia (Lat. *cirrus*, a tuft of hair ; *pes*, a foot) and is associated with a fixed or sessile habit of life. After passing through a variety of free-swimming larval forms the animal comes to rest and attaches itself by the anterior end of the body to a stone or rock, the bottom of a ship, or some other object submerged in the sea, and then becomes adult.

Like that of the Ostracoda the body of a Cirripede is enclosed in a carapace consisting of two valve-like folds which have grown out from the region of the head, but these are usually strengthened

by five calcareous plates, a right and left scutum, a right and left tergum and a median carina, and in *Balanus*, the common acorn-barnacle of our sea-shores, a further armour of triangular plates develops in an additional outer fold of skin which encircles the body. In *Lepas*, the barnacle which is usually found in clusters

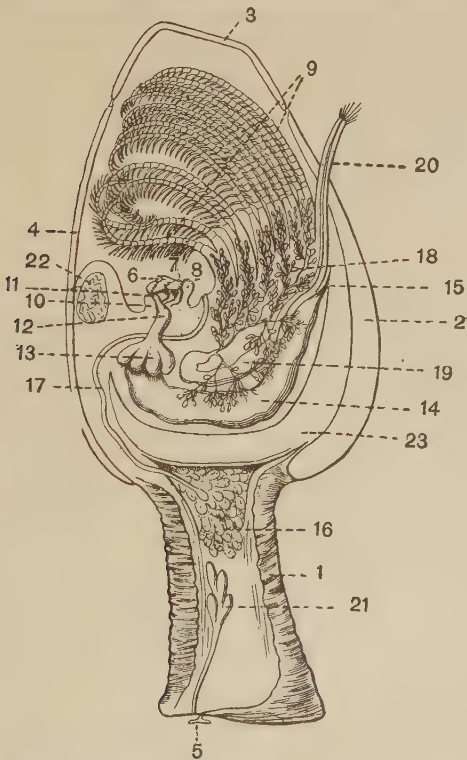

FIG. 83. A view of *Lepas anatifera*, cut open longitudinally to show the disposition of the organs. From Leuckart and Nitsche, partly after Claus.

1. Stalk. 2. Carina. 3. Tergum. 4. Scutum. 5. 1st antennae. 6. Mandible with "palp" in front. 7. 1st maxilla. 8. 2nd maxilla. 9. The six pairs of biramous thoracic limbs. 10. Labrum. 11. Mouth. 12. Oesophagus. 13. Liver. 14. Intestine. 15. Anus. 16. Ovary. 17. Oviduct. 18. Testes. 19. Vas deferens. 20. Penis. 21. Cement gland and duct. 22. Adductor scutorum muscle, which closes the carapace. 23. Mantle cavity, i.e., the space intervening between the carapace and the body.

on the bottom of ships, and which often seriously impedes their progress, this ring is absent, but the anterior end of the head bearing the first antennae at its end has grown out into a long stalk which lodges some of the internal organs of the body. The second antennae though present in the larvae are lost in the adult. The rest of the

body is enclosed within the carapace. Around the mouth are a pair of mandibles and two pairs of maxillae, and the thorax carries six pairs of biramous many-jointed limbs beset with numerous hair-like spines, the lashing of which kicks food particles towards the mouth (Fig. 83). These limbs are slender and flexible and thus differ from the corresponding limbs of Copepods.

Like some Copepods the Cirripedes are without a heart, and the existence of special respiratory organs is doubtful. Unlike other Crustacea they are, as a rule, hermaphrodite, the male and female reproductive organs being united in one individual. A few species are parasitic, chiefly on other Crustacea, and these have reached a very extreme stage of degeneration.

Sub-class B. MALACOSTRACA.

The second of the two large groups into which the Crustacea are divided contains most of the more familiar forms, such as Crabs, Lobsters, Shrimps, Wood-lice, etc. For the most part the Malacostraca are larger than the Entomostraca and the number of their segments is a fixed one. In all except the first order, Leptostraca, which is really a connecting-link between true Malacostraca and the lower forms, the number of segments is nineteen and there are nineteen pairs of appendages. One of the most marked characters in the Malacostraca is the differentiation of the trunk into two distinct regions, the thorax and the abdomen. It is true, as is mentioned above, that many authors speak of an abdomen in the Entomostraca, but by this they mean the hindermost segments which with a few exceptions are devoid of limbs. In any Entomostracan if we examine the series of limbs behind the jaws we shall find that they constitute a continuous series without any sudden change in their character. In a Malacostracan, on the other hand, we find an abrupt change at one point in the character of the limbs. The hinder limbs or swimmerets (pleopods) are markedly different from the front limbs, for whereas in the swimmeret both forks of the limb, endopodite and exopodite, are equally developed, in the last five pairs of limbs of the thorax (peraeopods) the endopodite is large and the exopodite is small or absent. It is this difference in character which defines the thorax from the abdomen.

Although the division between the head and thorax is not always apparent, as a rule we may assign five segments to the head, eight to the thorax and six to the abdomen, which ends in an unsegmented flap called the telson. The reason for this want of a definite boundary between head and thorax in the Malacostraca is

that the carapace, which as we have seen is an outgrowth of the head, has become fused with the dorsal surface of the thoracic segments, whilst at the sides it forms freely projecting flaps, which since they cover the gills are known as branchiostegites (Gr. στέγω, to cover).

The excretory organ of most of the Malacostraca opens at the base of the second antennae and not as in the Entomostraca on the second maxilla. As a rule the typical larva—the Nauplius—of the last-named group is not present in the life-history of the Malacostraca, which may hatch out from the egg in a practically adult condition or may pass through several larval stages, the first of which is the Zoaea, a larva with many appendages, possessing eyes and in all ways more differentiated than the Nauplius.

Order I. **Leptostraca.**

The order Leptostraca (Gr. λεπτός, slight, small) contains but three genera, which are interesting because they form an intermediate stage between the Malacostraca and the Entomostraca. Like many of the latter they are provided with a bivalve carapace which, unlike that of all other Malacostraca, is not fused with the thoracic segments. Behind the six appendage-bearing segments of the abdomen there come two more segments without limbs and the hindermost bears two diverging filaments constituting a "caudal fork," such as is commonly found amongst the Entomostraca. The thoracic limbs are flattened and leaf-like, as in *Apus*, but the mandible bears a three-jointed feeler or palp and the eyes are stalked,—both, on the whole, Malacostracan characters. The excretory organ opens on the second antenna, but in the larva the shell-gland or maxillary excretory organ is found and traces of it exist in the adult.

The order is marine, and very widely distributed throughout the ocean. Its members are capable of living and thriving in very foul water, so foul as to be fatal to most other animals. *Nebalia* is the best known genus.

Order II. **Thoracostraca.**

The Thoracostraca (Gr. θώραξ, a breast-plate) form a large group and contain many very different forms. They are placed together because the carapace has become fused with several of the thoracic segments, so as to form a region known as the cephalothorax, the exoskeleton covering which is not jointed and is not bivalved as in *Nebalia*. The eyes of the Thoracostraca are compound and almost always are borne on movable stalks. The order is divided into four sub-orders.

Sub-order 1. **Schizopoda.**

This sub-order includes the lowest of the Thoracostraca. The name is suggested by the circumstance that all the eight pairs of thoracic limbs are biramous; the first and sometimes the second pair are reduced in size and provided with gnathobases; they assist the mandibles and maxillae and hence are termed maxillipedes. It will occur to most observers that the thoracic feet of the Schizopod resemble the ordinary form of swimmeret or abdominal appendages in the more familiar Lobster or Crayfish. This is so; the swimmerets of a Schizopod are however sharply distinguished from the thoracic limbs by their smaller size. It appears probable that the first step in the evolution of an abdomen was the reduction in size of the appendages so as to transform the hinder

FIG. 84. *Nyctiphanes norwegica*, a Schizopod. Slightly magnified. From Watasé. The black dots indicate the phosphorescent organs. The gills are seen between the cephalothoracic and the abdominal appendages.

part of the body into a powerful steering fin or rudder, and many Schizopods only use the abdomen in this way, since most of the swimmerets are very small and appear to be practically functionless. The last one however is broad and assists the tail in its vigorous strokes. Some Schizopods have a series of phosphorescent organs which under certain conditions emit a pale but very perceptible light like that of a glow-worm. This light seems to be controlled by the animal but its use is not very clear.

There are very interesting differences amongst the genera composing the Schizopoda. The genus *Euphausia* for instance has long feathery gills attached to the basal joints of the thoracic legs and the eggs are not borne about by the mother but hatch out into Nauplii, which pass through a series of metamorphoses before becoming adult. In *Mysis* on the other hand the gills are few and simple and the eggs are borne under the thorax on flat plates termed oostegites, which project inwards from the hinder thoracic

appendages. In these two genera we see the beginning of two tendencies which have led the descendants of primitive Schizopoda to differentiate themselves in two different directions. One group have taken to carrying the embryos about until they are fully developed; at the same time the gills are reduced and the carapace, which is essentially a gill-cover, tends to disappear. This group includes the Stomatopoda, Cumacea and Arthrostraca.

In the other group the gills and carapace are retained, and though the eggs are for a time carried about attached to the swimmerets the young one passes through a larval stage before becoming adult. This group includes the Decapoda.

Dr Calman, one of the greatest authorities on Crustacea, divides the Schizopoda into two divisions, one division including *Mysis* and its allies, which he classes along with Arthrostraca as Peracarida, and another division including *Euphausia* and its allies, which he classes with the Decapoda as Eucarida. The Peracarida are distinguished by having oostegites and a liver consisting of few tubules, the Eucarida on the other hand carry the eggs attached to the swimmerets and have a liver of many tubules. There is however much convenience in grouping together all the low forms as Schizopoda, for which reason the name is retained here, although undoubtedly *Mysis* shows us the beginning of the type of structure which culminates in the Wood-lice, and *Euphausia* is not very different in essential structure from the lowest Shrimp.

Sub-order 2. **Decapoda** (Eucarida).

The Decapoda (Gr. δέκᾰ, ten) derive their name from the circumstance that the first three pairs of thoracic appendages have become maxillipedes, that is to say have been modified so as to assist in mastication, leaving five pairs of large conspicuous limbs, which have lost all trace of an exopodite, for prehension and locomotion.

This group includes the Lobsters, Crayfish, Shrimps, Prawns, Hermit-crabs and Crabs, etc. In the division of the Crabs, the Brachyura (Gr. βρᾰχύς, short; οὐρά, tail), the abdomen is reduced in size and turned up and closely applied to the under surface of the thorax, except when the animal is "in berry" and then the masses of eggs force the abdomen away from the thorax. The last appendages of the abdomen constituting the tail-fin have been totally lost; of the rest five pairs are retained by the female for the purpose of carrying the eggs, but in the male only the first two pairs, which are used for copulation, are retained. As a rule Crabs are broader than they are long and the breadth is partly due to the large gill

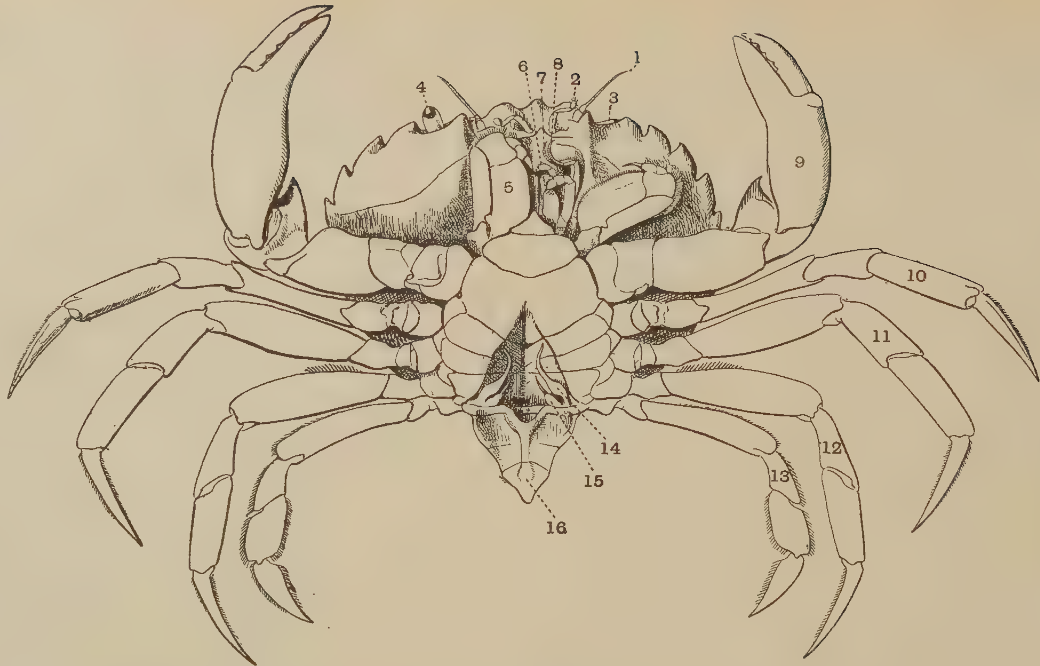

FIG. 85. *Carcinus maenas*, ventral aspect. The abdomen or tail is bent back. A little less than life-size.

1. Antenna. 2. Antennule. 3. Left eye reclining in its socket. 4. Right eye erected. 5. Right 3rd maxillipede in natural closed condition, its fellow is bent back to expose 6. 6. The mandible. 7. 1st maxillipede. 8. 2nd maxillipede. 9. Chela or great claw. 10, 11, 12 and 13. 1st, 2nd, 3rd and 4th ambulatory limbs. 14 and 15. 1st and 2nd abdominal legs which are modified in connection with reproduction. 16. Position of anus.

chambers on each side of the body. The gills of course are outside the body, but are in special chambers bounded by the branchiostegites or free edges of the carapace.

The Anomura are in some respects intermediate between the foregoing and the following division. As in the Crabs the

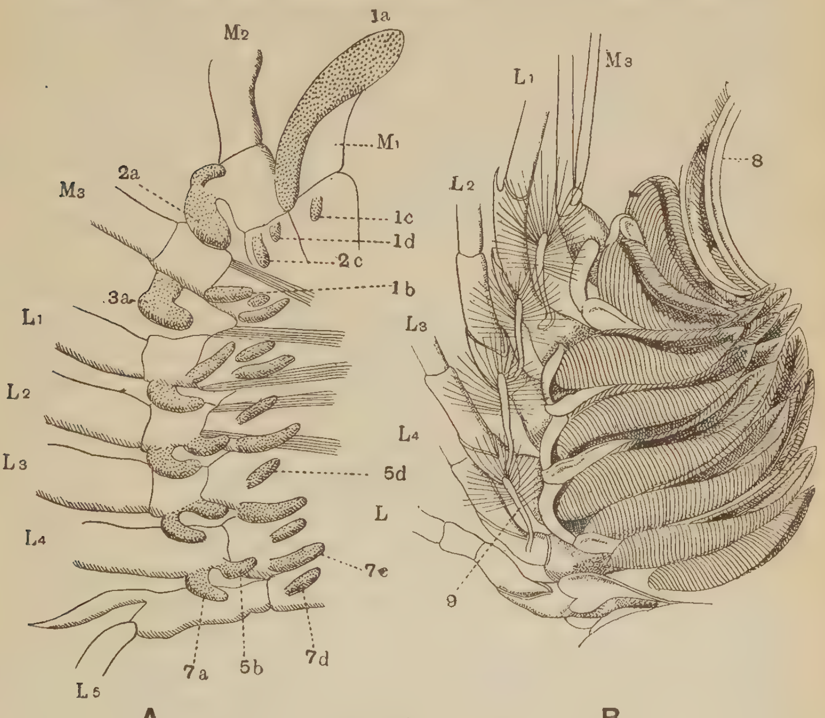

Fig. 86.

A. Left side of a larva of the Prawn, *Penaeus*, to show the origin of the gills. Slightly magnified. From Claus. L_1 to L_5. The first to fifth ambulatory limbs. M_1 to M_3. The first to third maxillipedes. 1a, 2a, 3a, 7a. Podobranchs. 1b, 5b. Anterior arthrobranchs. 1c, 2c, 7c. Posterior arthrobranchs. 1d, 5d, 7d. Pleurobranchs. Of these rudiments of gills only nineteen develop. B. Left side of a fully-grown Prawn, *Penaeus semiculcatus*, to show fully-grown gills. Slightly magnified. 8. Exopodite of second maxilla, which flaps to and fro and so causes a current over the gills. 9. Exopodite of fourth ambulatory limb.

abdomen is folded somewhat forwards but the tail-fin although reduced is retained. The last pair or last two pairs of the thoracic limbs are reduced and turned dorsalwards. Some species—the Hermit-crabs—shelter themselves in the empty shells of molluscs. In these cases the abdomen does not develop a hard covering, as the animal is sufficiently protected by its lodging. It remains soft

and acquires a spiral twist as it moulds itself to the interior of its borrowed shell.

In the Lobsters, Shrimps, etc., which form the division Macrura (Gr. μακρός, long; οὐρά, tail), the tail is relatively large and is not folded up against the thorax.

The group is for the most part marine, though the well-known fresh-water Crayfishes, *Astacus* in Europe and *Cambarus* in North America, form striking exceptions.

In the lowest family of the Macrura, the Penaeidae, vestigial exopodites are still retained on the thoracic limbs, and all four series of gills, pleurobranchs, anterior arthrobranchs, posterior arthrobranchs and podobranchs are well developed. These primitive Shrimps are very closely related to *Euphausia* and its allies amongst the Schizopoda.

Some Decapoda have left the sea and taken to living on land and this has in some cases involved a change of structure, the gills which breathe water being supplemented by the soft vascular lining of the gill-cavity covered by the branchiostegite which, like a lung, breathes air.

Sub-order 3. **Stomatopoda** (Hoplocarida).

The Stomatopoda (Gr. στόμα, a mouth) are a sharply defined group with few genera, and may be regarded as a peculiarly specialised offshoot from the primitive Schizopoda. The members attain a considerable size, some eight inches or more in length. The portions of the head carrying the eyes and antennules have become freely movable. The carapace is small and only covers the anterior five thoracic segments; the appendages of these segments are turned forward towards the mouth and take part in feeding, and so are termed maxillipedes. They end in a claw, the last joint shutting down on the penultimate one like a knife blade into its handle. They are thus very different from the maxillipedes of Schizopoda or Decapoda, which are really limbs on the way to become jaws and have developed gnathobases. The maxillipedes of Stomatopoda are grasping, not chewing organs, and have undergone the same modification as the great claw of the lobster, which might just as reasonably be called a maxillipede. A fertile source of confusion in the study of the Arthropoda is the use of names like maxillipede, thorax, abdomen, etc., to denote different things in different groups. The last three thoracic limbs are for walking; they are very feeble and retain a rudiment of the outer fork or exopodite. The

abdomen is large and bears six pairs of flattened swimming limbs, each of which carries a gill in its outer branch.

Unlike most other Crustacea, *Squilla* and the other members of the group do not carry their eggs about with them, but lay them in the burrows in which they live, and by sitting over them and moving their abdominal limbs they keep up a current of water which aërates the eggs. They are exclusively marine and live buried in the sand or hidden in crevices of the rock. They move actively and are difficult to catch.

Sub-order 4. **Cumacea** (Peracarida *pars*).

The members of the sub-order Cumacea (Gr. κῦμα, a wave, or billow) are mostly small; they live in the sea on sandy bottoms at considerable depths, but come to the surface at night. They are

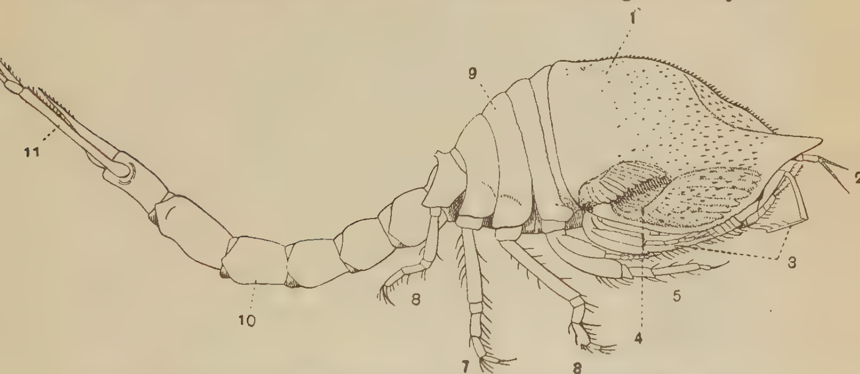

FIG. 87. Female *Diastylis stygia* × 6. After Sars. The carapace is represented as transparent to show the gill.

1. Carapace. 2. First antenna. 3. First leg. 4. Gill borne on first maxillipede. 5, 6, 7 and 8, second to fifth leg. 9. Free part of thorax. 10. Abdomen. 11. Appendage of the last segment of the abdomen.

especially interesting because to a certain extent they are intermediate in character between the Thoracostraca and the Arthrostraca. Thus their paired eyes are not stalked and are sometimes fused together to form a single eye; the carapace is reduced so as to leave several segments of the thorax uncovered (Fig. 87) and on some of the thoracic legs there is a small exopodite. They have a single pair of gills borne by the first thoracic limb—the so-called maxillipede. The exopodites of this pair of limbs lie in grooves running foreward on the surface of the head. They are folded into the form of tubes and convey away the water which has passed over the gills. In the female the abdomen, which is long, has lost all the limbs except the last pair. Like *Mysis* and its allies and like all the Arthrostraca they have oostegites projecting inwards from the bases of the thoracic limbs, which support the eggs.

Order III. **Arthrostraca** (Peracarida *pars*).

The members of the Arthrostraca (Gr. ἄρθρον, a joint; ὄστρακον, a shell) have sessile eyes, i.e., without stalks. The carapace, which in most of the above-mentioned groups covers the segments of the thorax, is absent, and consequently seven of the latter are usually freely movable on one another, the first and in rare cases the second thoracic segment remaining immovably fused with the head. They thus represent a further stage in the same process which we found going on in Cumacea and Stomatopoda. Only one of the thoracic appendages is modified so as to form a maxillipede; there are consequently seven pairs of walking legs attached to the thorax. In the female these legs bear oostegites which together form a floor to the brood pouch in which the eggs develop.

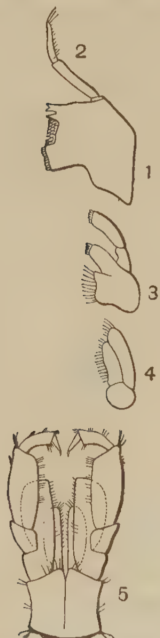

Fig. 88. The mouth appendages of *Gammarus neglectus*. From Leuckart and Nitsche, after G. O. Sars.
1. The left mandible.
2. Its palp.
3. 1st maxilla of left side.
4. 2nd maxilla of left side.
5. Maxillipede of each side together forming an under lip.

The Arthrostraca are mostly small animals, living in either salt or fresh water; they assume very different forms, some of them having a rudimentary abdomen. They are divided into the suborders Amphipoda (Gr. ἀμφί, on both ends; πόδα, feet), which are for the most part compressed or flattened from side to side (Fig. 89) and carry their gills on their thoracic appendages; the Isopoda (Gr. ἴσος, equal; πούς, ποδός, a foot), which are depressed or flattened from above downwards (Figs. 90 and 91) and whose gills are the modified endopodites of the appendages of the abdomen, and lastly the Tanaidacea a primitive group which are only slightly flattened, in which two segments are still attached to the head and there is a vestigial carapace sheltering an epipodite borne by the maxillipede. A typical example of the Isopoda is the Hog water-louse, *Asellus aquaticus* (Fig. 90), common in our ponds and streams, but many of the groups are parasitic and lose most of their characteristic Crustacean features.

As in the case of the Decapoda some genera of Isopoda have forsaken the sea for a life on land, amongst which the Wood-lice, *Oniscus* and *Porcellio*, exhibit certain peculiarities usually associated with Insects; thus the mandible has no palp, one pair of antennae is usually lost, and there are certain tubular air passages believed to be respiratory burrowed in the abdominal endopodites which recall by their structure the tracheae of air-breathing Arthropoda. This is another proof that any attempt to group together all animals possessing tracheae leads to absurdities.

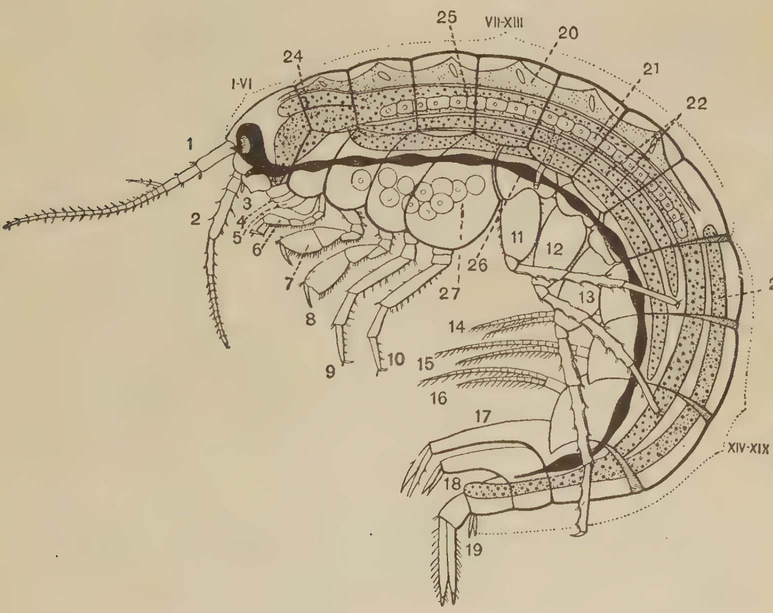

Fig. 89. *Gammarus neglectus.* Female bearing eggs seen in profile. From Leuckart and Nitsche, after G. O. Sars.

I–VI. Cephalothorax. VII–XIII. Free thoracic segments. XIV–XIX. The six abdominal segments. 1. Anterior antenna. 2. Posterior antenna. 3. Mandibles. 4. 1st maxilla. 5. 2nd maxilla. 6. Maxillipede. 7—13. Thoracic limbs. 14—16. Three anterior abdominal limbs for swimming. 17—19. Three posterior abdominal limbs for jumping. 20. Heart with six pairs of ostia. 21. Ovary. 22. Hepatic diverticula. 23. Posterior diverticula of the alimentary canal. 24. Median dorsal diverticulum. 25. Alimentary canal. 26. Nervous system. 27. Ova in egg pouch, formed from lamellae on the coxae of the second, third and fourth thoracic limbs.

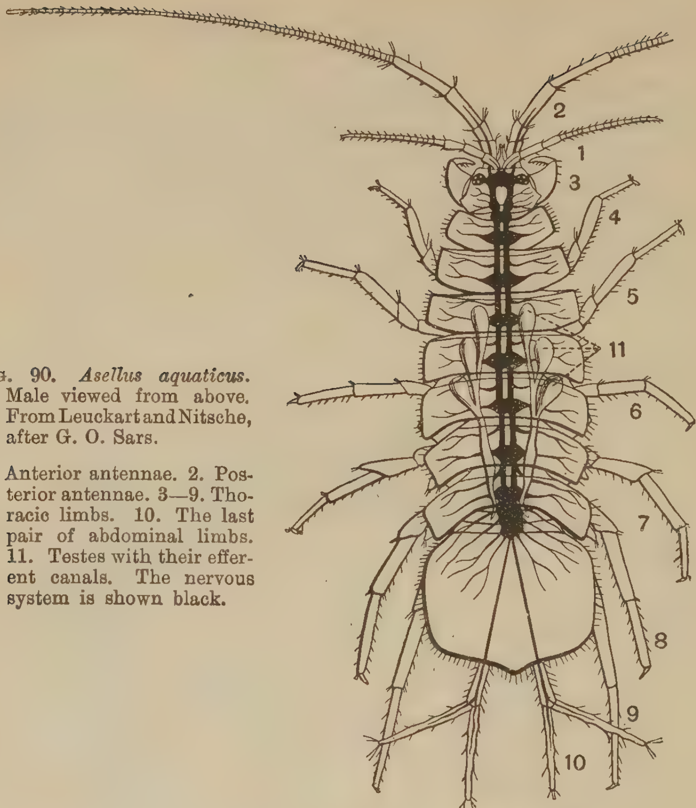

FIG. 90. *Asellus aquaticus*. Male viewed from above. From Leuckart and Nitsche, after G. O. Sars.

1. Anterior antennae. 2. Posterior antennae. 3—9. Thoracic limbs. 10. The last pair of abdominal limbs. 11. Testes with their efferent canals. The nervous system is shown black.

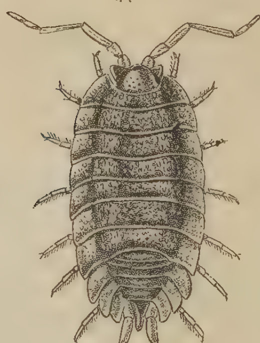

FIG. 91. A Wood-louse *Porcellio scaber* × about 2. From Cuvier.

Order IV. **Syncarida.**

A separate order is erected by Dr Calman to receive an extraordinary shrimp-like creature (*Anaspides*) found in mountain lakes in Tasmania which closely resembles some fossil forms from the

Carboniferous. The carapace is completely absent, the eyes are stalked and movable, the thoracic legs have oval exopodites formed with setae and each leg bears two epipodites which act as gills.

Class II. Antennata.

Sub-class A. Prototracheata (Onychophora).

A short account of these creatures all of which used to be included in the genus *Peripatus* must be given, as they are of a very primitive nature and in both their adult structure and the mode of its development throw much light upon the origin and anatomy of Myriapods and Insects and indeed on the Arthropods generally.

The different species of *Peripatus* are differently coloured, but they mostly possess a beautiful velvety coat. In shape they resemble caterpillars but carry two large antennae on their heads, and at the base of each antenna is an eye. On the under surface of the head is the mouth and tucked into it on each side is a toothed jaw. This is an appendage which has been modified so as to form a true gnathite. At each side of the mouth is a third pair of appendages, the oral papillae, from the tips of which a sticky slime can be ejected which entangles the insects and spiders on which the animal lives. The other appendages, which vary in number in the different species from seventeen pairs to over forty, have the form of soft cylindrical papillae ending in two claws and function as walking legs (Fig. 92). The anus is posterior, and at the base of each leg is a slit-like pore, the opening of an excretory organ. The genital pore is in front of the anus.

Fig. 92. *Peripatus capensis* × very slightly. From Sedgwick.

The body cavity is a spacious haemocoele divided into three longitudinal compartments by two bands of muscles which run from its outer upper angle towards the mid-ventral line. The lateral compartments are continuous with the cavities of the limbs and lodge the excretory organs which are coelomiducts but are usually termed "nephridia," the salivary glands and the nervous system. The alimentary canal, slime glands and generative organs lie in the middle compartment.

The mouth leads into a large muscular pharynx, such as is found in many Chaetopods. The salivary glands open near this. They

are interesting structures, since their development has shown that in origin they are homologous with the excretory organs. The pharynx leads by a short oesophagus into a roomy endodermic stomach which reaches back nearly to the anus, a short proctodaeum only being interposed (Fig. 93).

The structure of the heart and pericardium closely resembles that of the same organs in Myriapods and Insects.

The animal breathes by bunches of tracheae or short tubes which pass from the exterior into the tissues and convey air. Their external openings or stigmata are partly in two rows above and between the legs and partly scattered irregularly.

At the base of each leg is an excretory organ which ends internally in a vesicle. Embryological research has shown that this vesicle is a remnant of the true coelom which is spacious in the embryo, but becomes displaced as development proceeds by the haemocoele. Enclosed in the proximal part of the leg there is a gland called the crural gland.

Peripatus is bisexual, and again embryology has demonstrated that the cavity of the sexual organs is coelomic. The male deposits its spermatozoa in packets in the body of the female. It is not known how they reach the ova but they are usually found in the ovary and possibly bore their way through the tissues, as they do in some leeches. The ducts of the reproductive organs are, like the excretory organs, coelomiducts and belong to the same metameric series as the excretory organs.

The nervous system consists of a brain and two ventral cords, which however do not approach one another but lie wide apart. They are connected by nine or ten transverse commissures in each segment (Fig. 93). Posteriorly the two ventral nerve-cords fuse above the proctodaeum, an arrangement which recalls what occurs in certain primitive Mollusca.

There are many species of *Peripatus*, which are by some authorities grouped into three or four genera. They are found in widely separated parts of the world and afford, as is often the case with archaic animals, an excellent example of "discontinuous distribution." They have been found in South America and the West Indies, in South Africa, in Australia, New Zealand and in some of the islands of the Malay Archipelago and in Lower Siam.

The development of *Peripatus* first definitely solved the problem of the nature of the various spaces in the Arthropod body and has also thrown much light on some of the peculiarities of insect

embryology. One species lays eggs and the others produce living young.

That the animal is a most interesting "missing link" becomes evident if we attempt to sum up the Annelidan and the Arthropodan features of its anatomy. Thus *Peripatus* resembles Annelida in the nervous system, the muscular pharynx, the structure of the eyes, the serially repeated "nephridia," the shortness of the stomodaeum and of the proctodaeum, the thinness of the cuticle and the hollow nature of the paired appendages; but in the reduction in size of the coelomic spaces, the presence of a wide haemocoele and of tracheae, the nature of the antennae and of the heart and pericardium, the position of the genital pore and the presence of true gnathites, *Peripatus* approaches the Myriapods and Insects.

In habits these animals are shy and inconspicuous, hiding under bark or stones and preferring moist surroundings. They avoid the light and move with deliberation, testing the ground as they advance with their antennae.

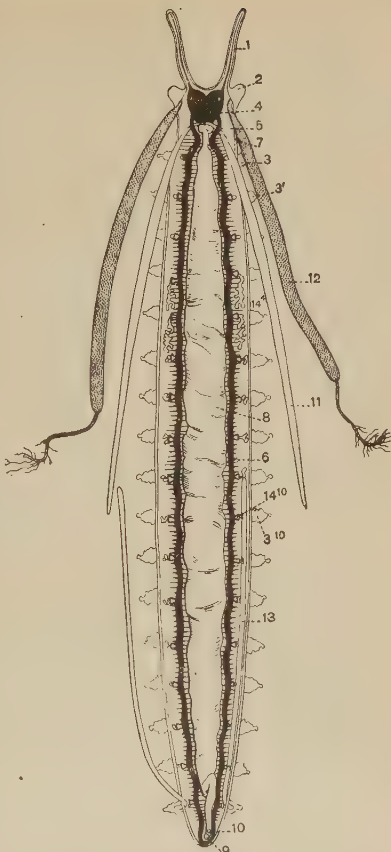

Fig. 93. *Peripatus capensis*, male, dissected to show the internal organs × 2. After Balfour.

1. Antennae, showing antennary nerve. 2. Oral papilla. 3, 3′, 3^{10}. 1st, 2nd and 10th leg of right side. 4. Brain and eyes. 5. Circum-oesophageal cord. 6. Ventral nerve-cord of right side, showing the transverse commissures. 7. Pharynx. 8. Stomach. 9. Anus. 10. Male generative opening. 11. Salivary glands. 12. Slime glands and reservoir. 13. Enlarged crural gland of the 17th leg. 14^4, 14^{10}. 4th and 10th nephridia of right side.

Sub-class B. Myriapoda.

The Myriapoda (Gr. μυρίος, countless) are characterised by the possession of a head distinct from the rest of the body, bearing antennae, mandibles and one pair of maxillae, followed by a large number of segments bearing simple leg-like appendages.

Compared with the Crustacea or Insecta the group is a small one, yet it contains some thousands of species which, if we except a few small animals, fall readily into two subdivisions (I) Chilopoda, and (II) Diplopoda. The subdivisions differ markedly from one another, especially in the position of their reproductive openings, which in the Diplopoda are on the third segment behind the head and in the Chilopoda are terminal. For this reason some naturalists break up the sub-class and associate the Chilopoda with the Insecta and the Prototracheata as Opisthogoneata we characterised by the posterior genital opening whilst the Diplopoda with two other orders consisting of minute degenerate forms are classed together as Progoneata.

Order I. **Chilopoda.**

The very active, lithe, chestnut-brown, rather fierce-looking little centipede, *Lithobius forficatus*, which is very common during the summer months under the bark of old trees, under leaves and other rubbish, is a good example of the Chilopoda (Gr. χίλιοι, a thousand) or Centipedes. In the winter it buries itself in the soil. The female lays her eggs from June till August and hastens to cover each with a thin layer of earth; otherwise the egg is seized and devoured by her mate.

External features.

If we examine a little more closely one of these Centipedes we shall see that the body is divided into a head followed by a very narrow segment and then by fifteen other segments of varying size. The head bears a pair of long antennae, the first appendages, which are constantly waving about. Close behind the point of origin of these antennae lie the eyes. If we turn the animal over and observe the under surface of the head we shall at once see a pair of large vicious-looking claws—the poison claws or fifth pair of appendages. The tip of each of these is perforated and, as it strikes the prey, a drop of poison is squeezed out which soon kills any insect or larva which the Centipede wishes to eat. The bases of these claws are produced into powerful gnathobases by which the prey is held. Although the tips of the poison claws are turned forwards beneath the head, yet these appendages really spring from the first segment of the trunk, which is enlarged and is known as the basilar segment. If we separate with a pair of

mounted needles these poison claws we shall see attached to the head the fourth pair of appendages, sometimes called the second maxillae, though they resemble legs and have undergone little modification. They are reduced in size and each has a blunt functionless gnathobase. In front of these the third pair of appendages or first maxillae take the form of a lobed plate, being united with one another in the middle line. These cover in their turn the second pair of appendages or mandibles which, like those of Insects and unlike those of Crustacea, consist simply of the blade, there being no palp or feeler.

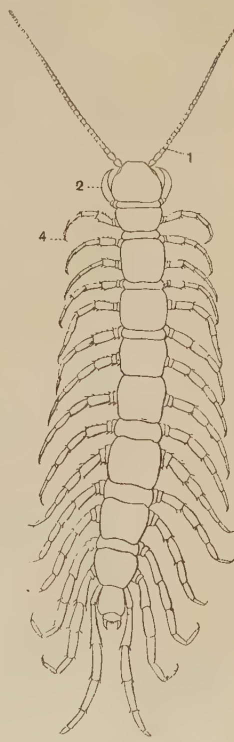

FIG. 94. A Centipede, *Lithobius forficatus*. Dorsal aspect × 12.

1. Antennae. 2. Poison claws (5th pair of appendages). 4. First pair of walking legs.

The fifteen segments which succeed the one carrying the poison claws each bear a pair of seven-jointed running legs ending in a pair of claws.

Internal structure.

Near the base of some of the legs—not of all—in the soft skin uniting the hard dorsal and ventral plates of chitin, is an oval opening. This leads into a chamber from which the tracheae pass off. These tubes divide and subdivide into smaller tubes, which run all over the body and traverse all the tissues, entering even the smallest cell. They are lined with a cuticle of chitin and are kept from collapsing by the presence of a fine spiral thickening of this cuticle which gives them a very characteristic appearance when seen through a microscope. They are full of air and constitute the respiratory apparatus of the Centipedes.

The existence of such a breathing apparatus, which is confined to Peripatus, the Myriapods, the Insects and certain of the Arachnids, is associated with certain striking features in the internal anatomy of the body. In most animals the oxygen of the air is taken up by the blood and carbon dioxide is given out at certain fixed points called gills or lungs, and the vascular system is arranged so as to drive the blood through these specialised respiratory

organs. The blood takes the oxygen to the various tissues and takes from them the carbon dioxide which is removed from the body at the same centres. In the Tracheata however the air is itself conveyed by means of the tracheae to all the cells of the body and the gaseous exchange takes place on the spot. The blood has in the Tracheata lost one of its chief functions, the respiratory one, and exists chiefly as a nutritive fluid bathing the alimentary canal and taking up from it the soluble food which it conveys to the other tissues. It is kept in circulation by a contractile heart which lies along the middle dorsal line of the animal. In *Lithobius* this heart has a pair of ostia or openings in each segment, into which the blood from the pericardium pours, only to be sent out of the heart again at its anterior end into the general cavity of the body, for here the heart has an opening and there is no system of smaller vessels or capillaries.

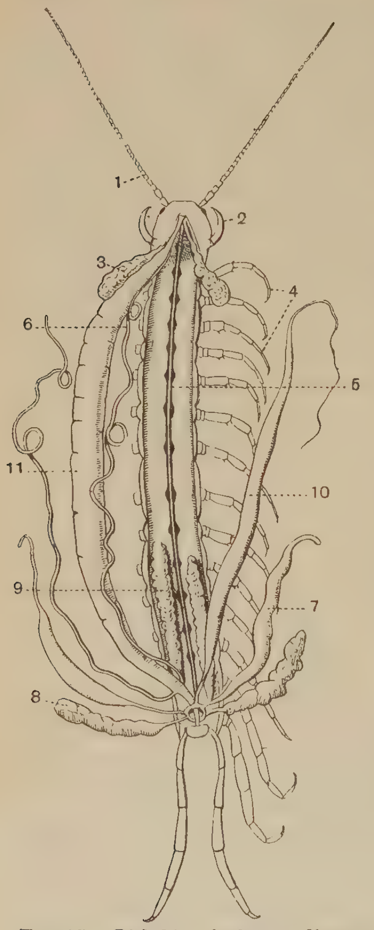

Fig. 95. *Lithobius forficatus*, dissected to show internal organs × about 2. After Vogt and Yung.

1. Antenna. 2. Poison claw. 3. Salivary gland. 4. Walking legs. 5. Ventral nerve-cord. 6. Malpighian tubule. 7. Vesicula seminalis. 8. Small accessory gland. 9. Large accessory gland. 10. Unpaired testis. 11. Alimentary canal.

One of the peculiarities associated with the above-mentioned method of breathing is the nature of the excretory organs which rid the body of its nitrogenous waste. In *Peripatus* we find more or less typical coelomiducts, and we meet with modifications of these in the coxal glands of some Arachnids, but in the Myriapoda and in the Insecta these organs are wanting and their place is

taken by certain outgrowths from the proctodaeum, called after an Italian anatomist Malpighian tubules. In *Lithobius* there are two such tubules, blind at their free end, and at the other opening near the hind end of the alimentary canal (6, Fig. 95). Their walls contain traces of uric acid and urates which they have taken up from the blood and which they presumably excrete through the alimentary canal.

The last-named organ is a straight tube which runs from one end of the body to the other. A pair of salivary glands pour their secretion into it near the mouth, but no other digestive glands exist. *Lithobius* is carnivorous, living chiefly upon insects, their larvae and earthworms.

A large part of the space in the head is occupied by the bilobed brain which supplies the antennae and the mouth appendages. This brain is connected by means of a nerve collar with a long ganglionated ventral cord which supplies nerves to the legs and the rest of the body (Fig. 95).

Centipedes are bisexual, the ovary and testis are continuous with their ducts which open to the exterior on the ventral surface of the last segment.

Order II. **Diplopoda.**

The second large subdivision of the Myriapoda is well illustrated by the black "Wire-worm," *Iulus terrestris*, very commonly found in Great Britain curled up under stones or burrowing in the soil, where

FIG. 96. *Iulus terrestris*, sometimes called the "Wire-worm." From Koch × about $3\frac{1}{2}$.

1. Antennae. 2. Eyes. 3. Legs. 4. Pores for the escape of the excretion of the stink-glands.

it is said to do much damage by gnawing the tender roots of plants, for all Diplopods (Gr. διπλόος, double) are vegetarians.

The Wire-worm is a black, shiny cylindrical animal with an enormous number of legs, in spite of which its movements are much slower than are those of *Lithobius*. The terga or dorsal shields are in this sub-group very much enlarged, whilst the sterna or ventral

shields are very much reduced, and thus it comes about that the bases of each pair of legs, instead of being separated by the width of the body, are close together. Another peculiarity in this sub-division is that each tergum corresponds with two segments and that each apparent segment bears two pairs of legs and has the internal organs also duplicated. This double arrangement however only begins at the fifth segment behind the head.

The appendages on the head are: (i) short, usually club-shaped antennae; (ii) mandibles; (iii) a single pair of maxillae fused into a lobed plate.

Both the first two segments behind the head bear but one pair of legs, the third has no legs but carries the openings of the generative ducts. Although oviducts and vasa deferentia are paired the ovary and the testis are single. Each consists of a large sac lying beneath the alimentary canal on the walls of which the genital cells are developed. The development shows that the sac is a remnant of the coelom. The fourth free segment has one pair of legs, the remainder two pairs.

The female *Iulus* lays her eggs, some 60 to 100, in an earthen receptacle she has prepared beneath the surface of the ground.

Sub-class C. Insecta.

The immense group of Insects far outnumbers in species any other group of animals and in all probability exceeds in number all the species of the rest of the animal world. New insects are constantly being discovered and although some quarter of a million have already been named and to some extent described, it is believed that at least as many more remain unrecorded.

In spite of these numbers Insects are as a whole a uniform group and show less diversity in size and structure than many of the smaller groups, as for instance the Crustacea or the Mollusca. Probably their great number and small range of structural variation is not unconnected with the fact that they have found a new medium in which to pass some part, at any rate, of their life. The other group of animals which have taken to flying and lead an aërial life—the birds—show a somewhat similar range of species accompanied by a uniformity of structure which in their case is even more marked.

External features.

Insects may be characterised by their body being divided into three distinct regions, the head, the thorax and the abdomen (Fig. 97). The head bears one pair of antennae and three pairs of gnathites. The thorax consists of three enlarged segments, each of which bears

on the ventral surface a pair of legs and the two hindermost of which bear on the dorsal surface a pair of wings. The abdomen consists of a varying number of segments, ten being perhaps the usual number but fewer often occur. The abdomen bears no appendages except at the posterior end, where a pair of rod-like outgrowths—the anal cerci—are often found.

Owing to the similarity of Insects to one another and their great number the study of them has become a very special branch of Zoology, which is termed Entomology. The necessity of extremely detailed study is due to the same cause and a great number of technical terms are in use for describing the numerous structures which build up the body of the Insect.

In this short book it will only be possible to indicate a few points about the anatomy of Insects and we shall take as a type the common cockroach because it is both a generalised form and not too small for dissection.

The common cockroach of the British kitchen is *Stylopyga orientalis*, but a larger form, *Periplaneta americana*, is often met with on ships and from them makes its way to the docks; it is also often found in zoological gardens, etc. *Phyllodromia germanica*, a small species, is becoming increasingly common in England.

The whole body of the cockroach is covered by a chitinous covering which varies in thickness, from the black hard head to the thin whitish areas which exist at the joints and which permit movement of the harder parts on one another. Except in the head the segments of the body can be detected externally, and, as in other members of the Arthropoda, the segmentation affects some only of the internal structures, such as the heart, the tracheae, the muscles and the nervous system, the other organs of the body not being influenced by it.

The head of a cockroach is a flattened structure placed at right angles to the axis of the body. It is oval in outline, its upper edge being considerably broader than the lower. It is loosely jointed to the thorax by a neck which permits considerable movement (Fig. 97). This neck enters the head near its upper edge and below it the head hangs free. On the upper and outer edge of the head are a pair of kidney-shaped, faceted eyes of a shining black colour, on the inner curve of which the antennae or feelers have their origin. These are long whip-like structures, often as long or longer than the body; they are made up of many joints and during life are in active movement, now stretched downward as if trying the

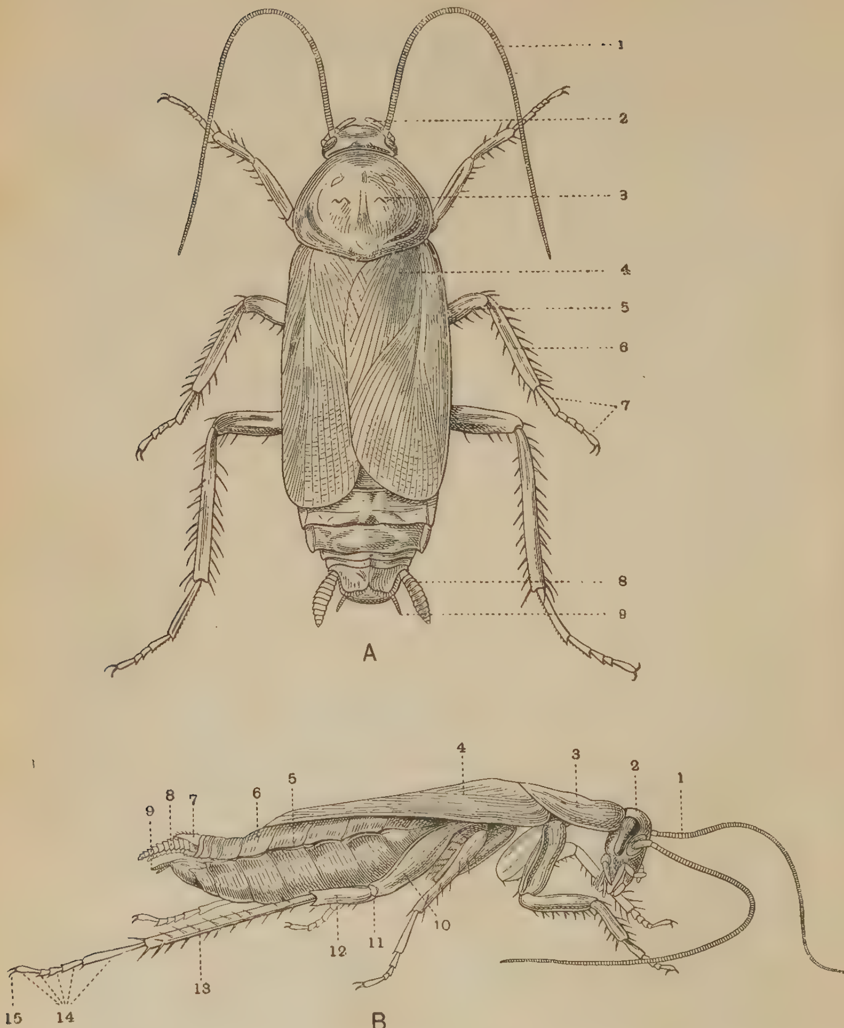

FIG. 97. *Stylopyga orientalis*, male × 2. A. Dorsal view. B. Side view. From Kükenthal.

A. 1. Antenna. 2. Palp of first maxilla. 3. Prothorax. 4. Anterior wings. 5. Femur of second leg. 6. Tibia. 7. Tarsus. 8. Cerci anales. 9. Styles.

B. 1. Antenna. 2. Head. 3. Prothorax. 4. Anterior wing. 5. Soft skin between terga and sterna. 6. Sixth abdominal tergum. 7. Split portion of tenth abdominal tergum. 8. Cerci anales. 9. Styles. 10. Coxa of third leg. 11. Trochanter. 12. Femur. 13. Tibia. 14. Tarsus. 15. Claws.

ground on which the creature moves and now waving aloft as if testing the air.

The mouth is on the lower edge of the head and is covered in front by a small movable flap called the labrum or upper lip. At the sides it is protected by the first and the second pairs of appendages, and behind by the fused third pair which form a plate called the labium, which completes the boundaries of the mouth behind (Fig. 98, C).

Mouth appendages.

If the first pair of mouth-appendages or mandibles be removed from the head and examined through a lens, each is seen to be a single-jointed stout jaw with a toothed inner edge which bites against the corresponding part of its fellow. It is characteristic of the mandibles of all Antennata

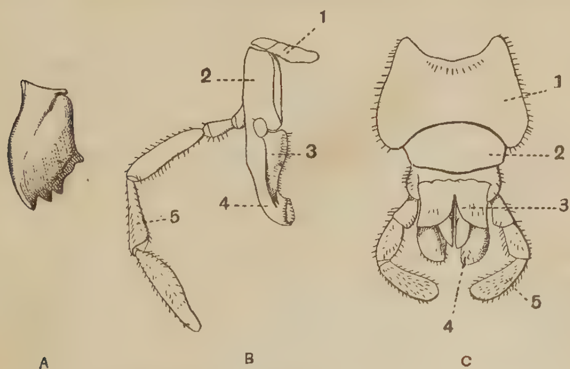

FIG. 98. Mouth-appendages of *Stylopyga*. Magnified.

A. Mandible. B. 1st maxilla. 1. Cardo. 2. Stipes. 3. Lacinia. 4. Galea. 5. Palp. C. Right and left 2nd maxillae fused to form the labium. 1. Submentum. 2. Mentum. 3. Ligula, corresponding to the lacinia. 4. Paraglossa, corresponding to the galea. 5. Palp.

to have no palp or remnant of the distal joints of the limb, such as is almost universally present in Crustacea.

Behind the mandibles and like them situated on each side of the mouth, are the first maxillae. Each consists of a number of joints and each joint has a special name. Like the typical gnathite of other Arthropods we may regard them as consisting of a limb-like appendage with out-growths from the basal joints biting against corresponding processes—gnathobases—of the fellow appendage. There are two of these gnathobases, the hard pointed lacinia and an outer portion, the softer galea (4, Fig. 98, B). The lowest joints termed the cardo and the stipes form an

L-shaped hinge which, when opened out, protrudes the jaw. The outer portion of the first maxilla is many-jointed and is sensory in function, constantly touching and testing the ground as the animal moves about. It is called the **maxillary palp**.

The second maxillae are united across the median line and thus constitute a fold or plate called the **labium**, which bounds the mouth behind as the labrum bounds it in front (Fig. 98, C). Each half may be resolved into elements similar to those of the first maxillae, the fused basal joints of the pair of appendages form the **mentum** and **sub-mentum**, the galea being represented by the **paraglossa**, whilst the inner gnathobase corresponds with the **lacinia** and is termed the **ligula**. As in the case of the first maxilla the outer joints of the appendage which have a tactile function are termed the **labial palp**.

Thorax.

The thorax is built up of three segments, the **pro-**, **meso-** and **meta-thorax**. The skeleton of each segment consists of a dorsal hard piece, the **tergum**, united with a corresponding ventral piece, the **sternum**, by a soft intervening **pleural membrane**. The tergum of the first thoracic segment is clearly visible, but the meso- and meta-terga are concealed by the wings. The two pairs of wings are formed by folds of the skin arising from the terga of the meso- and metathorax respectively, and in a state of rest conceal the dorsal surface of the animal behind the prothorax. The front pair are termed **elytra**; they are hard and horny, one overlaps the other, and they probably serve more as protectors to the delicate hind wings than as organs of flight. The posterior wings are thin and membranous and are of greater area than the elytra, and they constitute the effective organs in the rare flight of the cockroach. At rest they are folded like a fan and concealed by the elytra. In *Stylopyga orientalis* the wings—as is not uncommon amongst Insects—are rudimentary in the female.

The ventral plate or **sternum** of each thoracic segment bears a pair of legs by means of which the cockroach scuttles rapidly about.

Each leg consists of a number of joints, viz., a thick flat **coxa** applied to and articulating with the sternum; a minute triangular joint, the **trochanter**; a stout joint called the **femur**; a more slender one termed the **tibia**, armed with spines; then a piece consisting of five short joints called the **tarsus**, with a whitish hairy patch under each joint which acts as a sole; and finally a pair of terminal claws (15, Fig. 97, B). These names, as is too often the case

in Zoology, were suggested by fanciful and misleading comparisons with the parts of the limb of a vertebrate.

Abdomen.

The abdomen consists of ten segments and here the terga and sterna can be easily seen as they are not obscured by the insertion of the wings and legs. The eighth and ninth terga are however both tucked under the seventh and are not readily seen until the animal is artificially stretched. The tergum of the tenth or last segment stands out from the hind end of the animal and is cleft into two lobes. The sterna are equally distinct but the first is small. The abdomen is broader in the female than in the male, and the seventh sternum is shaped like the bow of a boat and projects backwards, hiding the posterior sterna and supporting the lower surface of a roomy pouch or cavity in which the egg-case is formed. In the male the seventh sternum conceals the eighth and ninth.

The stigmata leading to the tracheae are placed in the soft pleural membrane connecting terga and sterna.

The abdomen is usually regarded as being without appendages, but a pair of jointed cerci anales emerge below the edge of the tenth tergum in each sex, and in the male the ninth sternum bears a pair of anal styles. The claim of these structures to be reckoned as appendages of the same rank as the antennae, the gnathites and the legs, was at one time not generally conceded, but appears to be now fairly well established for the cerci anales.

In the soft tissue between the tenth tergum and the last visible sternum, at the hind end of the body, is placed the anus, and below it the single genital pore is situated. The anus is supported by certain thickened plates in the skin, known as podical plates, and around the genital orifices are arranged certain rods and bars, symmetrical in the female but asymmetrical in the male, termed gonapophyses, whose functions and meaning are obscure, but which are connected with the processes of copulation and of egg-laying. As we have seen, this region is in the female enlarged into a genital sac by the growth and modification of the seventh sternum and the tucking into the space so formed of the skin carrying the eighth and ninth sterna. The opening of the oviduct is on the eighth sternum and on the ninth is the single opening of the receptaculum seminis or spermatheca, which consists of two pouches of unequal size composed of inturned ectoderm: these are always found full of spermatozoa in the fertilised female. The spermatozoa apparently leave the spermathecae when the eggs are

being laid and fertilise the ova whilst they are in the genital sac. Two glands, consisting of branching tubes,—called colleterial glands—open separately behind the spermatheca. They secrete a fluid which hardens to form the egg-capsule in which the eggs are laid. This is moulded in the genital sac and may often be seen half-protruding between the distended seventh sternum of the mature female.

Internal structure.

When the skin is removed from the dorsal surface of the cockroach the cavity laid open is not a coelom but a haemocoele, and it is largely filled by a loose white tissue, known as the fat-body, which surrounds the various internal organs. If the alimentary canal be disentangled from this it is at once evident that in Insects, unlike other Arthropods, the intestine is longer than the body and the larger portion of it which lies in the abdomen is coiled in order to stow it away. Like the digestive tube of other Arthropods a large part of its length consists of the stomodaeum and proctodaeum. The former consists of an oesophagus which quickly passes into a large crop in which the food is stored for a time. The lining of both these regions bears hairs and the muscles in their walls are striped. The crop is followed by a gizzard, which bears internally six hard chitinous teeth, and behind them are fine hairs which act as strainers, so that only finely divided food can pass on into the mesenteron or chylific ventricle, as the part of the alimentary canal is called which alone is lined by endoderm and is capable of absorbing nourishment. This tube is produced in front into seven or eight pouches, the so-called hepatic diverticula. The mesenteron, the limit of which is marked by the insertion of the Malpighian tubules, is succeeded by the intestine or proctodaeum, a long coiled tube which enlarges posteriorly and opens by the anus. The enlarged portion is called the rectum (Fig. 99), the anterior coiled portion the colon.

Lying along the crop on each side are a pair of branched glands —the salivary glands—and a bladder termed the salivary reservoir. All three are provided with long ducts. Those of the two glands on each side unite to form a single tube which then receives the duct of the reservoir, and the common ducts of the two sides open behind the mouth but in front of the second maxillae. The saliva converts starch into sugar. The secretion of the hepatic diverticula emulsifies fats and turns insoluble proteids into the soluble forms (peptones). This secretion seems to pass forward into

the crop and there true digestion is effected. The digested and dissolved food then passes through the filter of the gizzard into the mesenteron, where absorption of the nutritious parts is effected, the undigested portions passing on to the intestine and so out of the body. The cells of the mesenteron undoubtedly exert some action on the products they absorb, though we are ignorant of its precise nature, but in the end they pass on the products of digestion—

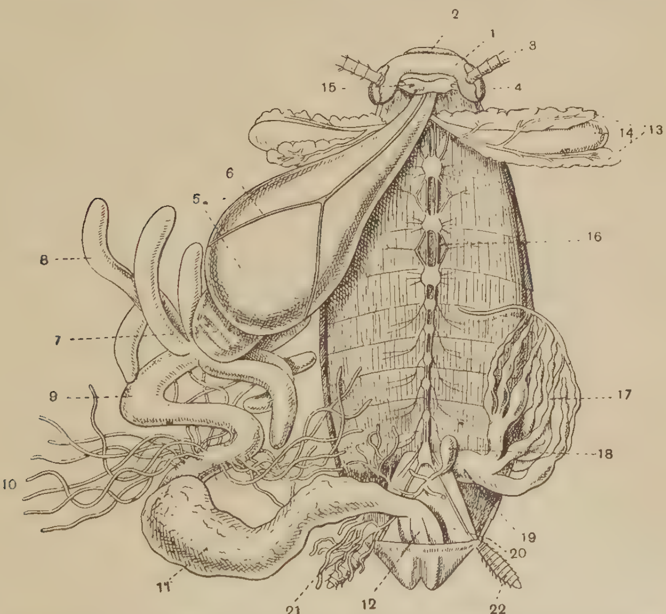

FIG. 99. A Female Cockroach, *Stylopyga*, with the dorsal exoskeleton removed and dissected to show the viscera. Magnified about 2.

1. Head. 2. Labrum. 3. Antenna cut short. 4. Eye. 5. Crop. 6. Nervous system of crop. 7. Gizzard. 8. Hepatic caeca. 9. Mid-gut or mesenteron. 10. Malpighian tubules. 11. Colon. 12. Rectum. 13. Salivary glands. 14. Salivary receptacle. 15. Brain. 16. Ventral nerve-cord with ganglia. 17. Ovary. 18. Spermatheca. 19. Oviduct. 20. Genital pouch in which the egg-cocoon is found. 21. Colleterial glands. 22. Anal cercus.

altered no doubt—to the blood which everywhere bathes the alimentary canal, and by it the new material is conveyed all over the body.

The blood is kept in circulation by the heart which lies in the mid-dorsal line close under the skin; in fact it can be seen through the skin in the region of the abdomen. It is a long vessel made up of thirteen chambers corresponding with the three thoracic

and ten abdominal segments, each chamber opening into the one in front and the whole somewhat resembling a row of funnels fitted one into another. At the broader hinder end of each chamber is a pair of ostia or holes through which the blood enters from the pericardium, and there are valves which prevent the blood being forced out of the ostia or forced backward when the heart contracts, so that its only course is to flow forward. The pericardium is separated from the rest of the haemocoele by the pericardial septum, in which however there are certain holes which permit an interchange of contents between the two cavities. When at rest the pericardial septum is arched upwards, but it is pulled outwards and flattened by the periodic contraction of certain muscles attached to its sides called the alary muscles, thus enlarging the pericardium and causing an inflow of blood into it from the rest of the haemocoele. This blood enters the heart when it is relaxed and the ostia are open, and hence by the alternate contractions of the alary muscles and the muscular wall of the heart the circulation is maintained.

The anterior end of the heart, called the aorta, opens by a trumpet-shaped orifice into the haemocoele and the blood pours out of this and bathes all the organs of the body. It thus takes up the soluble food which has left the alimentary canal and conveys it to those parts of the body where it is needed, and in a similar way it yields up its superfluous fat to be stored up in the fat-body and gives up its waste nitrogenous materials to the Malpighian tubules, whence they are passed out of the body. The haemocoele, especially in the abdomen, is largely blocked by a peculiar development of connective tissue, the cells of which are gorged with drops of fat and which is consequently white and opaque. It is this tissue which is termed the fat-body.

The heart contracts almost as frequently as the normal human heart, i.e., about seventy-two times a minute when the cockroach is at rest, but at other times its rate of contracting varies a good deal. The blood is colourless and contains amoeboid cells. It is slightly alkaline.

It is obvious from the above account that in the cockroach the blood is mainly a means of conveying nutriment to the organs and of taking certain waste matter from them, and that unlike what is usual in other animals, its respiratory function is at a minimum. Owing to the nature of the tracheae, the air with its oxygen is taken directly to each organ, almost to each cell, without the intervention of the blood.

The tracheal system opens to the outer air by ten pairs of oval pores or stigmata. These lie in the soft integument between the terga and sterna, one pair just in front of the mesothorax, one pair just before the metathorax and eight pairs just in front of each of the first eight abdominal segments, so that they seem to be intersegmental in position. These openings lead into tubes or tracheae which soon bifurcate and divide. The larger branches have a definite and symmetrical arrangement. There are dorsal arches running up towards the heart and ventral arches descending towards the nerve-cord. These arches are connected with one another longitudinally by trunks which run on each side of the pericardium and the nerve-cord. Large trunks also are given off to the alimentary canal It follows that should one stigma become blocked the organs which its tracheae supply are still provided with air. The finer branches become smaller and smaller until they become veritable capillaries which penetrate every tissue.

The tracheae being full of air present a glistening silvery appearance which is unmistakable. They are prevented from collapsing by the presence of a spiral thickening of the chitinous lining which runs round the interior of the tube just as the wire spiral strengthens the india-rubber tube of some kinds of garden hose. Respiration is effected by the alternate arching up and flattening of the abdomen, resulting in an alternate increase and diminution of its volume, which, since the blood is incompressible, secures an alternate inrush and expulsion of air from the tracheae. In all probability only the contents of the larger tracheae are affected by this process; by diffusion the oxygen from this "tidal air" is handed on to the finer tracheae.

In Insects the tracheal mode of respiration reaches its highest development and it is accompanied by a correlative diminution and simplification of the circulatory apparatus, the oxygen of the air being conveyed directly to and the carbon dioxide removed directly from the cells to the outer air, whilst the blood loses its respiratory function. It is doubtful how far this state of things is connected with the peculiar disappearance of the coelom—which presumably exists only in the cavity of the reproductive organs—because a similar replacement of the coelom by a haemocoele is found in Crustacea and Mollusca, where the blood is respiratory and the gills are compact and active organs; but probably it is correlated with the modification which the excretory system undergoes and this again is undoubtedly influenced by the state of the body-cavity.

Peripatus, the most primitive Arthropod, has in each segment excretory organs in the form of coelomiducts, each of which opens internally, not into a general coelom, but into a small sac which is really a special part of the coelom not communicating with any other coelomic space but belonging only to the excretory organ which opens into it. The main body-cavity is a haemocoele. Mollusca also retain a pair of such coelomiducts or in the case of *Nautilus* two pairs. These organs open into special coelomic spaces which are as a rule small, the more spacious cavities of the body being haemocoelic. Crustacea also retain coelomiducts, those of the fourth segment—shell glands—being persistent in the Entomostraca, whilst those of the second segment—green glands—persist in the Malacostraca. It seems probable that the sacs at the inner ends of these glands represent coelomic spaces. But even amongst Crustacea, in certain Amphipods for instance, we find the transference of the function of the coelomiducts to outgrowths of the alimentary canal. In Arachnids the coelomiducts or coxal glands show very varying degrees of development, but on the whole they are tending to die out and to be replaced by Malpighian tubules or diverticula of the intestine. Finally in Myriapods and Insects, where the true coelom is reduced to its minimum and where the tracheal mode of respiration attains a very high degree of development, all traces of coelomiducts have disappeared and the waste nitrogenous matter is excreted solely by the Malpighian tubules.

These are very fine long blind tubes, so fine as to be but just visible to the unaided eye, 60—80 in number, arranged in six bundles which open into the beginning of the narrow part of the proctodaeum from which they are outgrowths. They float in the blood, winding about amongst the abdominal viscera (Fig. 99). They contain crystals, probably of urate of soda, which are taken up from the blood and which leave the body through the intestine.

The nervous system of the cockroach is constructed on the same plan as that of the other segmented Invertebrates with which we have had to do. There is a large supra-oesophageal ganglion or brain giving off commissures, which encircle the oesophagus and unite below in a sub-oesophageal ganglion. Together these occupy a considerable portion of the cavity of the head. The supra-oesophageal ganglion supplies paired nerves to the eyes and to the antennae and is thus the sensory centre. The sub-oesophageal ganglion supplies the mandibles and both pairs of maxillae. From

it two cords pass backward and bear three pairs of ganglia in the thorax and six in the abdomen. This difference between the number of nerve ganglia and the number of segments is carried to a much greater extent in some Insects where, as in Spiders, all the post-oesophageal ganglia tend to fuse into a common nervous mass in the thorax (Fig. 107).

The only specialised sense organs are the eyes and the antennae. The eyes have fundamentally the same structure as those of the Crustacea: the antennae are the seat of the senses of smell and taste, and are in addition very delicate tactile organs. The maxillary palps are also tactile and are constantly touching and testing the ground on which the cockroach is moving.

Reproduction.

Cockroaches are bisexual. The ovaries in the female consist of two sets of eight tubes; each tube has developed from a coelomic sac in the embryo. They unite at their anterior ends into two cords which pass to the dorsal wall of the thorax and become attached to the pericardial septum, and at their posterior end they fuse into two short oviducts which join to form a small uterus (Fig. 99). Each of the sixteen tubes contains cells, some of which become ova, and as they approach the oviduct the ova become arranged in a single row. At the same time they increase greatly in size by the deposition of yolk in the egg, so that an ovum just before it leaves the body is of considerable size.

The eggs are apparently fertilised after leaving the uterus by spermatozoa which emerge from the spermatheca (in which they have been deposited by the male) situated behind the opening of the uterus. Whilst still in the genital pouch the fertilised eggs are surrounded by the secretion of the colleterial glands which open behind the spermatheca, and this secretion hardens into the egg-capsule or c o c o o n.

The paired testes of the male are functional only during youth and as they diminish in size after they cease to function, they are only to be found with difficulty. They lie concealed by the fat-body below the terga in the region of the fourth, fifth and sixth abdominal segments. They look somewhat like elongated bunches of cherries, their translucent colour strongly contrasting with the opaque white of the fat-body. Two vasa deferentia lead from the testes to a pair of large reservoirs called vesiculae seminales, which together form the "mushroom-shaped gland." Into these at an early age the cells destined to form spermatozoa pass from the testes and there they undergo their further development. The mushroom-shaped

gland opens to the exterior by means of a short muscular tube, the ductus ejaculatorius, which has its orifice just below the anus. The name of the gland is derived from its form; it has a thick stalk surrounded by a crown of branches. Fertilisation and oviposition take place during the summer.

Sixteen eggs are laid in each egg-capsule, and for some seven or eight days, until the mother finds some warm and secluded hiding-place to deposit her load, she carries about the capsule half-protruding from the genital pouch. When the embryos in the eggs are fully formed, which takes about twelve months, it is said that they secrete some fluid, probably saliva, which dissolves the upper part of the capsule and so permits of their escape. In *Phyllodromia germanica* the mother is said to take a part in freeing her offspring from their temporary imprisonment. When they first appear they are white with dark eyes, but the integument soon thickens and darkens. They have no wings, but in other respects they resemble their parents and thus there is no metamorphosis such as occurs in the Butterflies and many other Insects. They run actively about, devouring any starchy food they can find, and when in time they grow too large for their coat of mail it splits and a soft cockroach extricates itself therefrom. The integument soon hardens again. This casting of the skin or ecdysis takes place seven times, and after the seventh moult, when the insect is four years old, it is adult.

The Insects are subdivided into orders, which are mainly based (i) on the structure of the gnathites; (ii) on the nature of the wings; (iii) on the amount of metamorphosis which the life-history of the Insect presents. A short account of each of these criteria is therefore subjoined.

The Mouth-Parts (Gnathites) of Insects.

The mouth-parts of Insects can in almost all cases be resolved into a pair of mandibles which never bear palps and two pairs of maxillae which are usually provided with palps. There is present in the embryo in addition a pair of vestigial appendages situated behind the mouth. These in many insects coalesce to form the tip of a spine-like structure termed the hypopharynx. In the different orders of Insects and in different members of the orders these mouth-appendages show many modifications and are put to a very great variety of uses. One or other part may be suppressed and disappear, others may coalesce, as is the case with the right and left

second maxillae of the Cockroach, but as a rule traces of all the gnathites may be found though often much altered. The mouth-parts of Insects have been grouped as follows: (i) *Biting*. This kind of mouth is found in the Aptera, the Orthoptera, the Neuroptera and the Coleoptera (v. below), in which orders there is as a rule no very great difficulty in recognising the various parts which have been described in the Cockroach. As an example of the great variety presented by the mandible, those of the male Stag-beetle, *Lucanus cervus*, may be mentioned. In this animal the mandibles may equal in length the whole of the rest of the body. (ii) *Sucking*. This kind of mouth is found in the Lepidoptera or Butterflies. Here the mandibles are rudimentary, but the laciniae of the first maxillae are much elongated; each lacinia is grooved and so applied to the other as to form a tube, and in some cases the two halves of the tube are locked together by minute hooks; this tube is generally coiled into what is sometimes termed the proboscis. The palp of this maxilla is absent or rudimentary. The labium composed of the second maxillae is an important structure in the larva or caterpillar, as it forms the spinnerets through which the silk of the cocoons is excreted, but in the adult it is represented only by its palps which persist as large hairy structures. The hollow tube formed by the maxillae is well adapted to suck up the fluids on which the Lepidoptera live. The suction is performed by a powerful muscular sac called the suctorial stomach, which is a lateral outgrowth of the oesophagus and communicates with it. (iii) *Piercing and Sucking*. The Diptera or Flies possess both sucking and piercing organs, which are as a rule somewhat unequally developed. The basal portion of the labium or second maxillae is much elongated and takes the form of a fleshy protuberance which to some extent ensheaths the other parts. In the House-fly, *Musca domestica*, the piercing organs have been lost, but in the Gnat or Mosquito they reach a high degree of development. These parts are overlaid by a somewhat enlarged labrum and between this and within the grooved labium the pointed stylets lie. The hypopharynx* is well developed and is easily distinguished since it takes the form of a sharp style. Two pairs of lateral stylets, identified by some as the modified mandibles and first maxillae, also exist and the maxillary palp acts as a sensory organ. The Hemiptera or Bugs have a very similar set of gnathites in correspondence with their habit of boring into animals or plants to feed on their juices. In this

* See page 257.

order the mouth-parts when not in use are bent under the body and lie along the under surface of the thorax. The labium is jointed and its edges are curved so as to form an incomplete tube, only the base of which is partly covered by the labrum. Within this groove four sharply pointed styles—the mandibles and first maxillae—work. There are no palps. (iv) *Biting and Sucking.* The Hymenoptera or Bees and Wasps have mandibles not unlike those of a Cockroach and use them for biting and moulding their food (pollen) and the wax they secrete from their bodies. The laciniae of the maxillae form blade-like structures and their palps have much diminished in size. The labial palps however are large, and the conjoined median outgrowths from the labium (corresponding to the ligula of the Cockroach, 3, Fig. 98, C) form a kind of grooved tongue along which the nectar in the flowers is sucked up.

It thus appears that although the mouth-parts of Insects are highly modified in connection with the kind of food they live on and the modes in which they obtain it, nevertheless the various mouth-parts have a common ground plan, and although the authorities differ as to details, a fundamental similarity runs through these appendages in the different orders.

Wings of Insects

The wings of Insects are folds of the integument, flattened so that the two sides are in contact on their inner surfaces. At certain places however slits are left and through these tracheae pass taking air to the wings. The cuticle of both upper and under layers is also thickened along certain lines and the presence of these thickenings divides the wing up into a number of areas. These lines are usually called wing-veins or wing-nerves, but as they are neither veins nor nerves it is better to call them **nervures**. The presence and disposition of the nervures is of the highest importance in classification. Wings may be thin, membranous, and transparent, as in the Grasshopper (Fig. 100) and Dragon-fly (Fig. 74), where there are an enormous number of nervures, or in the Flies and Bees, where there are few nervures, or they may be thickened and strongly chitinised as in the front wings of Beetles. In this last group the anterior wings are called **elytra** (Gr. ἔλυτρον, a cover) and they always meet together in a median longitudinal line, so that when they are closed the insect appears to be wingless

(Fig. 101): in some few cases they have fused together so that the posterior or flying wings are rendered useless. In one great division of the Hemiptera one half of the anterior wing is horny and strongly chitinous, the other and posterior half membranous. In the Cockroach, as we have seen, the anterior wings tend to

FIG. 100. *Pachytylus migratorius.* A Grasshopper. Natural size.

become horny and are of little use in flight (Fig. 97). The posterior wings of the same insect when at rest are folded together something like the leaves of a shut fan and many species in several of the orders fold up their hind wings when not in use. The tucking away of these wings under the small elytra is a complicated affair in some Insects such as the Earwig, where the nippers at the end

of the body are said to aid in the process. Many Insects however, such as the Dragon-flies, Plant-lice, Butterflies, Moths, Flies, Bees and numerous others, do not fold up their wings but either bear them erect or lying depressed on the body In some cases the wings are quite transparent, but in the Moths and Butterflies they are covered with a dense fur of flattened scales which can readily be brushed off as a fine powder or dust (Fig. 104). It is these scales which give rise to the beautiful and in some cases gorgeous colouring of the Lepidoptera.

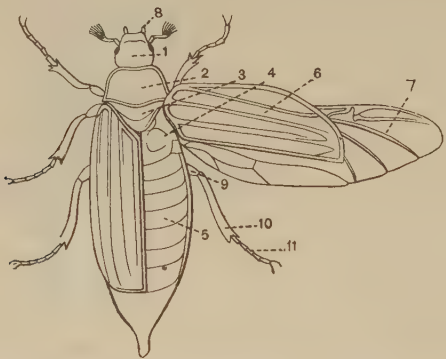

FIG. 101. A Male Cockchafer, *Melolontha vulgaris*, seen from above and slightly enlarged. After Vogt and Yung.

1. Head, stretched forward. 2. Prothorax. 3. Mesothorax, 4. Metathorax. 5. Abdomen. 6. Anterior wing (elytron) of right side, turned forward. 7. Posterior wing of right side, expanded. 8. Maxillary palps. 9. Femur of third right leg. 10. Tibia of third right leg. 11. Tarsus of third right leg.

Two pairs of wings are present as a rule, but the order Diptera has only the anterior pair, the hind wings being replaced by certain stalked structures called balancers or halteres. In the Hymenoptera, the two wings of each side are clamped together by means of hooks on the hind wing which fit into a ridge on the hinder edge of the front wing (Figs. 108, 109, and 110) The two wings of each side thus move as one. It is not uncommon to find isolated species in which the wings are not developed, for instance, the females of many Plant-lice and some Moths; while Fleas, which used to be placed amongst or near the order Diptera, which now are classed by themselves as Siphonaptera, never possess wings, though their absence is compensated for by a special development of the powers of jumping.

Metamorphosis.

A very large number of animals that live in the water, whether in the sea or fresh water, hatch out from the egg in a larval condition. That is to say, the being which leaves the egg is very unlike the adult in structure and habits, but by growth and a series of accompanying changes, in time passes over into the adult which is capable of reproducing. These changes constitute the metamorphosis. In the life-history of land animals such larval stages are rare and indeed hardly exist outside the Insecta and the Amphibia. As we have seen, the egg of a Cockroach gives rise to a young Cockroach which differs but little from the adult and gradually grows into it by a series of small changes, but which never at any time undergoes a long period of profound rest. But if we consider the case of a Moth or Butterfly we shall find that the egg does not give rise to an animal resembling a minute Butterfly but to a worm-like larva or caterpillar, which has no wings and in other respects is very unlike the Insect which produced the egg. This caterpillar as a rule eats voraciously and grows rapidly with little change in form until its fourth ecdysis, when a sudden change occurs, and the so-called pupal stage supervenes. In this stage with a few exceptions the animal, now called a pupa (Lat. *pupa*, a puppet), is motionless and ceases to feed. It may be uncovered and protected only by the hardened integument or it may be enclosed in a casing or cocoon. In the case of the Silkworm Moth and some others, this is constructed of silk. During the pupal stage, the animal undergoes a profound change, many of its organs and tissues being broken up and new ones constructed. When this process is completed the pupa casts its skin, makes its way out of the cocoon and emerges as an imago (Lat. *imago*, an image) or perfect insect.

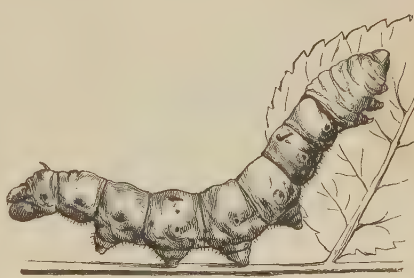

FIG. 102. Larva of *Bombyx mori*, the Silkworm. Life size.

The various orders of Insecta differ in the degree to which metamorphosis occurs. In the Aptera there is no metamorphosis and the development is said to be direct. In Orthoptera and

Hemiptera there is no quiescent pupa stage and the chief difference between the larva and adult is the absence of wings in the former. Here the metamorphosis is said to be incomplete. The same is true of Ephemeroptera, Isoptera and Paraneuroptera. Amongst the Lepidoptera, Coleoptera, Hymenoptera and Diptera there is a well-marked pupal stage, and these orders are said to have complete metamorphosis. Various names have been given to the larvae of Insects without very precise definitions. Those of the Lepidoptera are usually called Caterpillars. They are often gaudily coloured and bear tufts and bunches of hair. Besides the three pairs of legs which are found on the three segments following the head and which correspond with the legs of the imago, certain of the abdominal segments bear fleshy stumps called abdominal legs. The larvae of some of the Saw-flies (Hymenoptera) have a similar bright colouring and resemble Caterpillars, and like them feed exposed on leaves, etc. The larvae of Beetles and most Hymenoptera are as a rule hidden underground or in galls or wax-comb. They are whitish in colour and unattractive, and are often

FIG. 103. Cocoon of *Bombyx mori*, from which silk is spun. About life size.

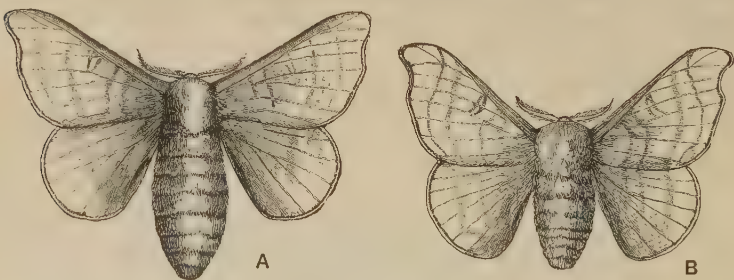

FIG. 104. Silk-worm moth, *Bombyx mori*.
A. Female. B. Male.

termed grubs, whilst the footless white larvae of the Diptera, which are for the most part deposited in some organic substance—whether alive or not—are usually called maggots. The wingless young of Orthoptera and of the other orders in which incomplete metamorphosis occurs are termed nymphs.

In the following account of Insect Classification we can only indicate the chief characters of each order and mention the names of one or two common members of each.

Order I. **Aptera.**

Wingless Insects, with scales and hairs covering the body. The mouth-parts are adapted for biting. They move by running or by springing by aid of a caudal style which is kept bent forwards under the abdomen and retained in this position by a ventral hook. When released from this hook the recoil of this style hurls the insect into the air. The segments of the thorax are not fused together and there is no metamorphosis.

Not all wingless Insects belong to this order. The name Aptera (Gr. ἄπτερος, wingless) refers to the belief that the ancestors of these Insects never had wings and that thus they represent a lower stage of evolution than the rest of the sub-class.

For the most part the Aptera are minute Insects living in retired spots under leaves or rubbish, in roof-gutters, etc., but they are widely distributed over the world. One of the best known is the Silver-fish, *Lepisma*, which hides in disused cupboards, old chests of drawers, sugar barrels, etc. It runs with great rapidity. *Machilis* is a small insect found between tide marks in seaweed. In it the abdominal exponents have small vestigial appendages.

Order II. **Orthoptera.**

The Orthoptera (Gr. ὀρθός, straight; πτερόν, a wing) have mouth-parts adapted for biting. The anterior wings are as a rule stiff, and when the Insect is at rest one overlaps the other, and both usually cover and conceal the large membranous hinder wings with which the creature flies. There is an incomplete metamorphosis, the young being at first without wings.

This order is a very varied one and doubts exist as to whether it is a natural one. It includes the Cockroach, whose anatomy has already been described; the Earwig, *Forficula*; the praying insect, *Mantis*; the leaf and stick insects, *Phyllium* and *Phasma*; the Grasshopper (Fig. 100), *Pachytylus*; the Locust, *Locusta*; the Cricket, *Gryllus*; and many others.

Order III. **Paraneuroptera**, or Dragon-flies.

The Paraneuroptera (Gr. νεῦρον, a tendon and hence a nervure) have biting mouth-parts. Both pairs of wings are membranous and used in flight, and the "veins" of the wings form a more or less close network. Metamorphosis is incomplete.

This order includes the Insects familiarly known as Dragon-flies. Two of the best known genera are *Libellula* and *Aeschna* (Fig. 74).

A number of other small orders of Insects agree with the Paraneuroptera in possessing two pairs of membranous wings with numerous nervures. These were formerly grouped with the Paraneuroptera in one large order termed the Neuroptera and this course was adopted in former editions of this book. Continued research has shown that amongst these "nerve-winged" insects profound differences occur both as to the character of the mouth-parts and the nature of the metamorphosis; and in consequence the old group of the Neuroptera has been divided up, and its divisions given the rank of orders. A few only of these orders will be mentioned here, viz.:

Order IV. **Ephemeroptera** or Day-flies.

In these Insects the nymph stage is passed in water and lasts a long time, in some cases as much as two years. Breathing is effected by the so-called tracheal gills—wing-like organs projecting from the sides of the abdomen in which tracheae ramify. These have been recently shown to be modified abdominal appendages. Oxygen diffuses from the water into the air in these closed tracheae and thence into the blood, instead of as in the gills of animals of true aquatic ancestry, directly into the blood. From this circumstance it is clear that the nymph represents a terrestrial not an aquatic ancestor. The imago takes no food, it emerges from the cuticle of the nymph in the evening and hovers over the water for a few hours during which time mating and laying of eggs is accomplished. The gnathites though vestigial are of the biting type. *Ephemera*, the May-fly, is the commonest British form.

Order V. **Isoptera,** Termites or White Ants.

In these Insects the gnathites are like those of the Cockroach, of a strongly marked biting type. They live in large colonies which include one perfect sexually developed female (the queen) and one ripe male at least, and a very large number of imperfectly developed wingless females which are divided into two varieties, termed respectively the workers with small heads and the soldiers with enormous heads and powerful jaws. They live on decaying wood and burrow in it, never exposing themselves to the light if it can be

avoided. Wings are only developed on the sexually ripe Insects at the time when they swarm out from the nests and when cross fertilisation can take place. Isoptera are confined to the tropics and are fearfully destructive of furniture, clothing, etc. Two forms, *Calotermes* and *Eutermes* come as far north as Sicily.

Order VI. **Thysanoptera**, or Corn-flies.

These are minute black Insects which infest flowers—including under that title the inflorescences of corn and other grasses. The wings are fringed with hairs The basal parts of the maxillae coalesce to form a tube. One mandible only is developed and this forms a curved stylet. The nymph resembles the adult except in possessing no wings, but a motionless pupal stage intervenes between larvae and adult forms *Thrips* is the common British genus.

Order VII. **Trichoptera**, or Caddis-flies.

In these Insects a sucking tube is formed by the coalescence of both pairs of maxillae and the mandibles are vestigial or entirely absent in the imago, so that as in Lepidoptera nutrition has to be obtained from such sources as honey, in which a preliminary stabbing of the host-plant is not required. The wings are covered with hairs, which may be compared to the scales on the Lepidopteran wing, since these latter are only flattened hairs. The larva resembles the larva of Ephemeroptera: it has biting mouth-parts and tracheal gills attached to the abdomen and is aquatic in habit. It constructs for itself a case of bits of stone or shell which ensheaths and protects the abdomen and which when larval life is over serves as a case to protect the pupal or motionless stage which intervenes between the larval and imaginal stages. *Phryganea* is a British example of this order.

Order VIII. **Neuroptera** (sensu stricto).

These Insects possess biting mouth-parts. The larvae are sometimes terrestrial and sometimes aquatic and in the latter case they possess tracheal gills which like those of Day-fly nymph are modified abdominal legs. The wings of the adult are devoid of hairs. There

is always a quiescent pupal stage: *Sialis* the Alder-fly, much used by anglers, *Myrmeleon* the Ant-lion, *Hemerobius* the Aphis-lion and *Chrysopa* the Golden-eye lace-winged fly are examples of this order found in Britain.

Order IX. **Coleoptera**

The Coleoptera (Gr. κολεός, a sheath) or Beetles have mouth-parts adapted for biting. The anterior wings termed elytra (sing. elytron) are hard and horny and meet in the middle line of the back in a straight suture and conceal the abdomen. The hinder wings are membranous and folded and used for flight. There is a grub-like larva with biting mouth-parts and a quiescent pupa which takes no food. The metamorphosis is consequently complete. This order has always been a favourite one with collectors, because its firm exoskeleton renders preservation and identification easy, and so the number of species of it named and described is much greater than in the case of any other order of insects. At least 90,000 species are known. One of the most familiar British beetles is *Coccinella*, the Lady-bird, in which the elytra are bright red in colour diversified by black dots; it is one of the greatest friends of the gardener, as it devours plant-lice.

FIG. 105. In the centre *Coccinella septempunctata*, the Lady-bird × about $2\frac{1}{2}$, with the larva to the left × about $2\frac{1}{2}$, and the adult beetle, natural size, to the right.

The so-called Black-beetle as we have already seen is not a Beetle at all but belongs to the Orthoptera, a much more primitive order. If for example we dissect one of our larger British beetles such as the Cockchafer or June-bug (*Melolontha*) and compare its anatomy with that of the Cockroach we cannot fail to be struck by the comparative specialisation of the former insect as compared with the latter. Thus in the Cockchafer the branches of the tracheae end in vesicles (Fig. 106), the Malpighian tubes are reduced to two which are beset with pouches; there is a huge tubular eversible organ, the penis, for transmitting the spermatozoa to the female, and the entire abdominal chain of ganglia is fused with and indistinguishable from the last thoracic ganglion (Fig. 107). The reader should compare with this the account given of the anatomy of the cockroach on pp. 233—244.

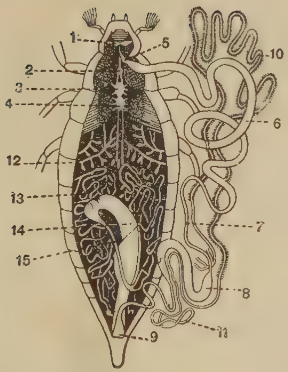

FIG. 106.

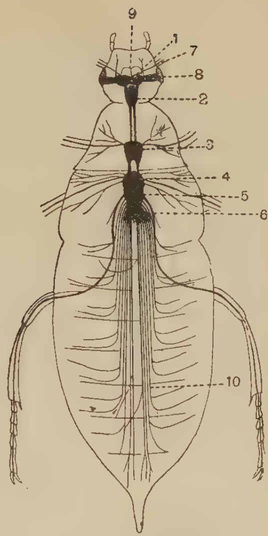

FIG. 107.

FIG. 106. View of male Cockchafer, *Melolontha vulgaris*, from which the dorsal integument and heart have been removed to show the internal organs. After Vogt and Yung.

1. Cerebral ganglion. 2. 1st thoracic ganglion. 3. 2nd and 3rd thoracic ganglia fused. 4. Fused abdominal ganglia. 5. Oesophagus. 6. Mid-gut. 7. Small intestine. 8. Colon. 9. Rectum. 10. Malpighian tubules, brown portion with caeca. 11. Malpighian tubules, distal end. 12. Trachea with vesicles. 13. Testes, opening into coiled vasa deferentia. 14. Penis. 15. Single vas deferens.

FIG. 107. View of nervous system of the Cockchafer, *Melolontha vulgaris*. After Vogt and Yung.

1. Cerebral ganglion. 2. Sub-oesophageal ganglion. 3. 1st thoracic ganglion. 4. 2nd thoracic ganglion. 5. 3rd thoracic ganglion. 6. Fused abdominal ganglia. 7. Nerves to antennae. 8. Optic nerves. 9. Origin of sympathetic nerves. 10. Abdominal nerves, a pair to each segment, which split into an anterior and posterior branch.

Order X. **Hymenoptera.**

The Hymenoptera (Gr. ὑμενό-πτερος, membrane-winged) have mouth-parts adapted for biting and sucking. The ligula of the labium is long and grooved, whilst the paraglossae are small. The mandibles are well developed and the laciniae of the first maxillae large. The four wings are alike, membranous in texture, but with vastly fewer nervures than the wings of insects belonging to the "Neuropterous" orders, and the hind wings are hooked on to the anterior in such a way that the two wings of each side move together. The metamorphosis is complete.

This group comprises the Ants, Bees and Wasps. Many of them live in highly complex communities, in which small sterile females act as "workers," and in their social habits and general intelligence they reach a level which is only surpassed by man him-

FIG. 108. *Formica rufa*, the Wood-ant.
1. Female. 2. Male. 3. Neuter.

Worker-bee. Queen-bee. Drone.
FIG. 109. *Apis mellifica*, the Honey-bee.

FIG. 110. *Polistes tepidus* and nest.

self. The group includes the Wood-wasp, *Sirex*; the Saw-fly, *Tenthredo*; the Gall-fly, *Cynips*; the *Ichneumon*; the Ant, *Formica*; the Wasp and Hornet, *Vespa*; the Humble-bee, *Bombus*; and the Honey-bee, *Apis*.

Order XI. **Hemiptera.**

The Hemiptera (Gr. ἥμι, half) have mouth-parts arranged for piercing and sucking. The basal part of the labium is elongated and tubular and the mandible and first maxilla form sharp pointed styles. The two pairs of wings may be alike or may differ and the anterior pair are in some cases half horny and half membranous. The metamorphosis is incomplete, there being no quiescent stage.

The members of this order present very great divergence both of form and of size; they are colloquially known as Bugs and Lice. Amongst the commoner forms are the Water-boatman, *Notonecta*; the Water-scorpion, *Nepa*; the Bed-bug, *Acanthia*; the *Cicada*, the "Cicala" of Italy, remarkable for its chirping noise; the Frog-hoppers, including the Cuckoo-spit, *Aphrophora*; the Plant-louse, *Aphis*; the *Phylloxera*, which destroys vines and Scale Insects from one of which the dye Cochineal is prepared.

Order XII. **Diptera.**

The Diptera (Gr. δι-πτερά, two-winged) have mouth-parts arranged for piercing and sucking. The chief difference in this respect from the Hemiptera consists in the fact that the sucking tube is partly formed by the labrum and that the first maxillae retain palps. In addition to the styles formed by the elongation of the mandibles and the laciniae of the first maxillae there is a fifth style, the hypopharynx, situated in the middle line which represents an elongated chin and carries the duct of the salivary gland. Only one pair of wings, the anterior, are present; the posterior are represented by a pair of short knobs called balancers or halteres (Fig. 112). The metamorphosis is complete.

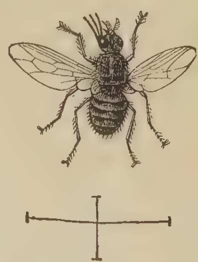

Fig. 111. *Glossina morsitans*, the Tsetse-fly.

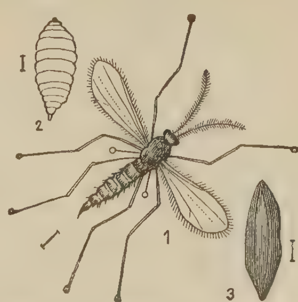

Fig. 112. *Cecidomyia destructor*, the Hessian-fly.
1. Insect. 2. Larva. 3. Pupa, or "flax seed." All magnified.

The Diptera or Flies form one of the largest of the Insect Orders, probably as large as the Coleoptera, although at present the number of species of Beetles named and

described is far greater than that of Flies. Amongst the commoner genera are the Gnats and Mosquitoes, *Culex*; the Daddy-long-legs, *Tipula*; the Gall-fly, *Cecidomyia* (Fig. 112); the Horse-fly, *Tabanus*; the Bot-fly, *Oestrus*; the common House-fly and Blue-bottle, *Musca*, and many others.

Order XIII. **Siphonaptera.**

The Fleas, of which the commonest is termed *Pulex irritans*, are wingless but endowed with considerable powers of jumping. They were formerly classed with the Diptera, but are now regarded as a type of a separate order, the Siphonaptera (sometimes called Aphaniptera).

In the Fleas the mandibles form stylets with saw-like edges and there is a short hypopharynx. The maxillary palps are long but the basal portions of these appendages are broad and triangular and not converted into stylets. The labial palps are very long and grooved and form sheaths for the mandibles and the hypopharynx. The metamorphosis is complete, the larva is worm-like and lives on animal refuse. The body of the adult is much compressed from side to side, which is an unique feature among Insects.

Order XIV **Lepidoptera.**

The Lepidoptera (Gk. λεπίς, a scale, πτερόν, a wing) have mouth-parts adapted for sucking only. The two pairs of wings are similar in appearance and covered with scales (flattened spines) which give rise to the beautiful pattern on the wings but are easily rubbed off. None of the wings fold up and when not in use are either held erect or are depressed on each side of the body. The metamorphosis is complete.

This order is very clearly defined and the members show a marked resemblance one to another. It includes the Butterflies and Moths, and all of them exhibit a very definite and complete metamorphosis. The eggs give rise to worm-like larvae known as caterpillars, which consume much food, generally of a vegetable nature (Fig. 102). After a considerable time, varying from a few weeks to three years, the caterpillar comes to rest, and in such cases as the Silk-worm Moth, *Bombyx mori*, surrounds itself by a case or cocoon spun by itself, which furnishes the material silk (Fig. 103). Within this cocoon, or in some species without forming a cocoon, the caterpillar forms a pupa, and whilst in this state it

undergoes a very thorough reorganisation and gradually the mature Insect is built up; after a certain time this emerges and occupies its comparatively short life in the propagation of its species (Fig. 104). The female usually deposits its eggs on or near the plants which serve as food for its offspring.

Class III. ARACHNIDA.

The third large group of the Arthropoda is a very varied one and contains many animals which differ markedly in their structure one from another. Perhaps the most distinctive features of the Arachnida (Gk. ἀράχνη, a spider; εἶδος, shape) are

External features.

(i) There are no true gnathites. No appendage loses all other functions and becomes exclusively a jaw, although the proximal joints of several are prolonged inwards towards the mouth and help to take up food; in a word some of the limbs have developed gnathobases; (ii) The most anterior appendages are never antennae but always a pair of nippers, termed chelicerae; (iii) The active catching and walking legs of the fore part of the body or prosoma are strongly contrasted with the plate-like modified limbs of the middle part of the body or mesosoma when the latter exist, but in many cases these have disappeared and in others have become so modified that they are no longer recognisable as limbs. Nearly all Arachnids moreover agree in having the anterior end of the body, the prosoma[1] as it is called, marked off from the rest and covered by a single piece, the carapace. The rest of the body or abdomen is in some forms differentiated into two regions, the mesosoma and metasoma, but in other cases this distinction does not exist; it may be segmented or it may not. The prosoma bears six pairs of appendages and of these the last four are usually walking legs. The appendages of the abdomen are connected with the respiratory function and are much modified, often—in the terrestrial forms—forming floors for the respiratory chambers. The breathing apparatus in the most primitive marine forms consists of gills. In the many land forms these gills are retained but are

[1] The name cephalothorax is often applied to this region, but the term is too misleading to be used. The cephalothorax of Decapod Crustacea includes the first thirteen segments of the body: the prosoma of Arachnida only includes six, and therefore corresponds roughly to the "head" of the higher Crustacea. Similar criticism might be launched against the use of the word "abdomen," but here the error is too deep-rooted for correction since the term is used in describing both Crustacea and Insecta, and in each case in a different sense.

enclosed in respiratory chambers. In other land forms tracheae assist the respiratory chambers and in still others entirely replace them. The gills have a peculiar form found only amongst Arachnida. They consist of "books" of thin superposed lamellae attached to the posterior aspect of an appendage. When modified for breathing air these "books" are called lung-books. When, as is the case in *Limulus*, they breathe oxygen dissolved in water they are called gill-books. The genital orifice is usually on the anterior end of the abdomen and ventral: the group is bisexual. Many different orders are included in the Arachnida, the best known being perhaps those which include the Spiders, the Harvestmen, the Mites and the Scorpions. The last named are found only in warm climates and Mites are too small for investigation with the naked eye, so that we shall take the Spider as an example of Arachnid structure.

Order I. **Araneida.**

Spiders belong to the Order Araneida (Lat. *aranea*, a spider), in which the abdomen is unsegmented and soft. The second pair

FIG. 113. The Garden Spider, *Epeira diademata*, sitting in the centre of its web. After Blanchard.

of appendages, the pedipalpi, are leg-like and modified in the male in connection with the fertilization of the female. The abdomen bears certain modified appendages called spinnerets, on which open the glands, the secretion of which produces the Spider's web. If we examine such a Spider as *Epeira diademata*, which is common enough in English gardens, sitting on or near its well-shaped web (Fig. 113), we notice that behind the prosoma there is a slender waist and that this is followed by a large swollen abdomen with no outward trace of division into segments, or into meso- and meta-soma.

External structure.

There are six pairs of appendages, and it is at once noticeable that there are no antennae or feelers to act as sensory organs. Their function is to some extent taken over by the long walking legs. The first pair of limbs are called chelicerae; in *Epeira* these are two-jointed, the terminal joint being pointed and folded down against the basal joint except when being used (Fig. 114). This pair of appendages contains poison glands and the poison escapes through an opening at the point of the second joint. By means of it the Spider can kill insects and seriously hurt larger animals.

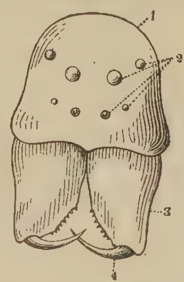

FIG. 114. Front view of the head of a Spider, *Textrix denticulata*. Magnified. From Warburton.

1. Head. 2. Eyes. 3. Basal joint of chelicerae. 4. Claw of chelicerae.

The second pair of appendages in the Arachnida are called pedipalpi (Fig. 115). In *Epeira* they resemble the walking legs, but in the male at the final moult the last joint becomes altered and forms a hollow sac—the palpal organ—which plays an important part in fertilizing the female.

Then follow four pairs of walking legs each with seven joints and terminated with two or three claws; in some species they are provided with a pad of short hairs called a scopula, which helps the animal to run on walls and ceilings.

The mouth is very minute, for the Spider does not swallow solid food but sucks the juices of its prey. It lies between the bases of the pedipalps, and the basal joint of each of these appendages has a cutting blade termed the "maxilla" (2, Fig. 115). It is a common feature of the Arachnids that the basal joints of one or more of the pairs of appendages develop gnathobases and act as jaws, but the modification never goes so far as to obscure

the limb-like form of the appendage and so produce a true gnathite.

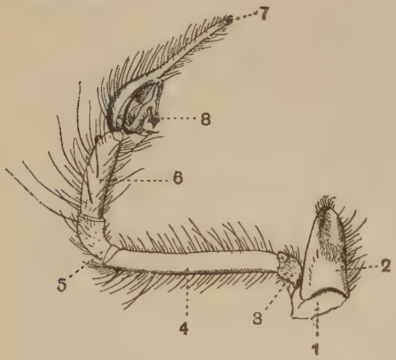

FIG. 115. Pedipalp of *Tegenaria guyonii*, the large house-spider.

1. Coxa. 2. Gnathobase, the so-called "maxilla." 3. Trochanter. 4. Femur. 5. Patella. 6. Tibia. 7. Tarsus. 8. Palpal organ.

On the ventral surface of the abdomen just behind the waist is situated the genital opening, protected by a plate; on each side of this is the slit-like orifice of a lung-book. The lung-books are very remarkable structures. Each opens to the exterior by a pore through which the air enters, and consists of a sac the cavity of which is largely occupied by a number of thin plates in the substance of which the blood circulates and is thus brought into close relationship with the air which passes in and out between the neighbouring plates; the sac is floored in by a special plate which is a modified appendage (Figs. 116 and 117). Such a breathing apparatus is peculiar to the Arachnida. In some Spiders we find a second pair of lung-books placed behind the others, and in other species this second pair is replaced by a pair of tracheae recalling the respiratory mechanism of the Myriapods or the Insects (Fig. 116). They have however been independently developed, and probably owe their origin to the sac of a lung-book from which the lamellae have disappeared. Certain branches of these tracheae situated near the middle line are believed to be modified tendons of the abdominal muscle, for in all Arthropoda the tendons of the muscles are formed by hollow involutions of the ectoderm lined by chitinous cuticle.

Spinnerets.

Near the hinder end of the abdomen are four tubercles or spinnerets, and if these be pushed aside, two more, shorter in length, come into view. These are the organs which form the web and they have been shown to be vestiges of abdominal appendages. They are very mobile and are pierced at their ends by hundreds of minute pores through which the silk exudes as a fluid, hardening on exposure to the air (18, Fig. 118).

The silk is secreted by a large number of glands which have their exit at the above-mentioned pores. Of these in *E. diademata* there are five different sorts and each secretes a special kind of thread; for the various lines in a Spider's web differ considerably one from another, in accordance with the use they are put to. The circular lines are sticky and help to catch insects for the Spider's food, the radial lines are stout and form a framework for

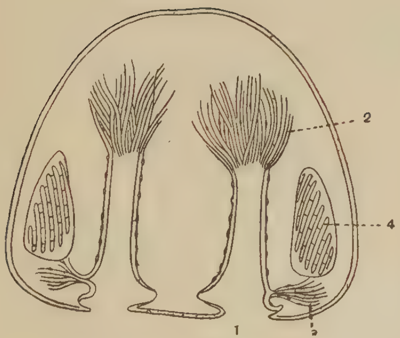

FIG. 116.

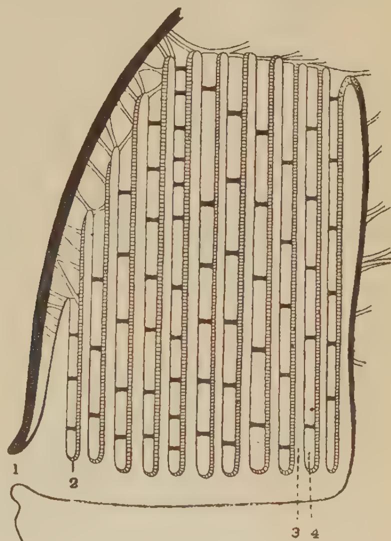

FIG. 117.

FIG. 116. Horizontal section through the abdomen of a Spider, *Argyroneta*. After MacLeod. Magnified.

1. Opening to exterior, tracheal stigma. 2. Terminal tracheae. 3. Lateral tracheae. 4. Lung-books.

FIG. 117. Longitudinal section through the lung-book of a Spider. Magnified. From MacLeod.

1. Opening to the exterior or stigma. 2. Free edge of the pulmonary leaves. 3. Space in which the air circulates. 4. Space in which the blood circulates.

the support of circular lines; the threads with which the Spider binds up its captured prey differ from these, and there is still another kind of thread with which it constructs its cocoons, and each kind of line is supplied from different sets of glands.

The dissection of a Spider requires much care, since the organs almost fill the body and are completely embedded in the large

masses of the digestive and reproductive glands. The oesophagus, which leads from the mouth, opens into a strong sucking "stomach," which, like the stomach of the Crayfish, is really a stomodaeum. This is attached by muscles to the chitinous exoskeleton, and when the muscles contract its cavity is enlarged and thus a sucking action is induced at the mouth (Fig. 118). Behind this is an endodermic portion of the alimentary canal which gives

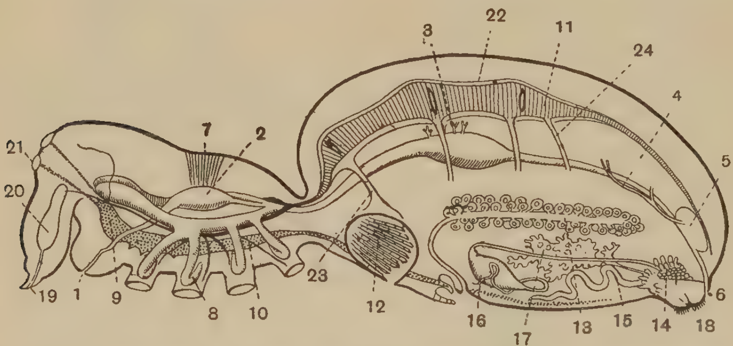

FIG. 118. Diagram of a Spider, *Epeira diademata*, showing the arrangement of the internal organs × about 8. From Warburton.

1. Mouth. 2. Sucking stomach. 3. Ducts of liver. 4. Malpighian tubules. 5. Stercoral pocket. 6. Anus. 7. Dorsal muscle of sucking stomach. 8. Caecal prolongation of stomach. 9. Cerebral ganglion giving off nerves to eyes. 10. Sub-oesophageal ganglionic mass. 11. Heart with three lateral openings or ostia. 12. Lung-book. 13. Ovary. 14. Acinate and pyriform silk glands. 15. Tubuliform silk gland. 16. Ampulliform silk gland. 17. Aggregate or dendriform silk glands. 18. Spinnerets or mammillae. 19. Distal joint of chelicera. 20. Poison gland. 21. Eye. 22. Pericardium. 23. Vessel bringing blood from lung sac to pericardium. 24. Artery.

off two caeca or blind tubes which project forwards; from each of these four smaller pockets arise one projecting into the base of each walking leg; behind these comes an intestine which traverses the abdomen and is further provided with a number of ducts which collect the products of a very capacious digestive gland or "liver." The hinder portion of this intestine is swollen up into a pouch called the stercoral pocket. Following the intestine comes a short proctodaeum lined by ectoderm which ends in an anus situated close behind the spinnerets.

Spiders possess two kinds of organs which excrete waste nitrogenous material: (i) the coxal glands, which are coelomiducts, like the "nephridia" of *Peripatus*, i.e., glandular tubes running between a reduced coelom and the exterior, and (ii) Malpighian tubules, a

pair of simple pouches opening into the endodermal intestine and thus in their origin differing from those of Insects. The coxal glands are better developed in some species, such as the common House-spider, *Tegenaria derhamii*, than is the case in *E. diademata*, where they are very degenerate and where their functions seem to have largely passed to the Malpighian tubules. In fact these structures are an interesting example of a set of organs degenerating and of their functions being assumed by another set.

The heart of the Spider is of the same general type as that of Myriapods; it is a tube with paired slit-like openings—ostia—at the sides, through which the blood enters to be driven out again through certain rather ill-defined vessels to circulate in the spaces between the various organs

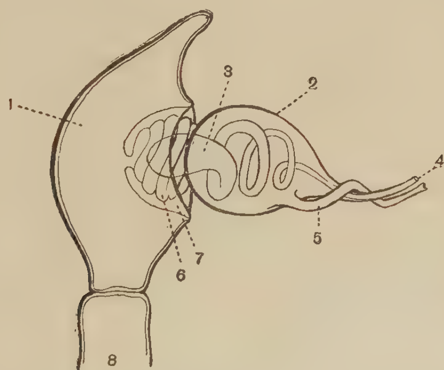

Fig. 119. Diagrammatic view of Palpal Organ.

1. Tarsus. 2. Bulb. 3. Vesicula seminalis. 4. Opening of vesicula seminalis. 5. Conductor. 6. Haematodocha. 7. Alveolus.

The nervous system is concentrated; there is a bi-lobed ganglion above the oesophagus which gives off nerves to the eyes and the chelicerae; this is connected by two lateral cords, which pass one on each side of the oesophagus, with a large nervous mass situated in the thorax. From this, nerves pass off to supply the remaining five pairs of limbs and two nerves arise which pass backward and supply the abdomen. The only conspicuous sense organs of Spiders are the eyes, which are "simple"; of these in *E. diademata* there are four large eyes arranged in a square on the top of the head and two small ones on each side of the square. This number, eight, is not uncommon in Spiders, where both the number of eyes and their disposition are much used in systematic classification.

The male, as is not uncommon amongst the Araneida, is smaller than the female. The ovaries and testes lie in the abdomen and have the form of a network of tubes, a form characteristic of Arachnida; the spermatozoa are conveyed to the palpal organs of the pedipalpi of the male and by them introduced into pouches, the spermathecae of the female. The palpal organ is a bulb-like outgrowth of the pedipalp or second appendage of the male. The base of the bulb, the so-called haematodocha, is elastic and marked by a spiral groove—it is attached to the terminal joint of the pedipalp in such a way that this joint partially ensheathes it forming a so-called alveolus round it. The bulb and its base, the haematodocha, contain a sac, the vesicula seminalis, which opens by a narrow duct on the apex of the pointed extremity of the bulb. This needle-like point is protected by a spiral outgrowth from the bulb coiled round it which is called the conductor. The male Spider deposits its seminal fluid on a web. It then inserts into this fluid the point of the bulb, the blood pressure in the pedipalp is then diminished and the diminished pressure causes the fluid to be sucked up into the bulb. When the male copulates the pressure in the haematodocha is increased and this forces the spermatozoa out into the genital opening of the female.

The eggs are fertilised before they are laid, which latter event usually takes place in October, when they are enclosed in cocoons of yellowish silk. The young are hatched out in the following spring and at once begin spinning. By means of the minute threads they secrete they weave a kind of nest about the size of a cherry-stone which hangs suspended from some twig or leaf. At the least disturbance the hundreds of young spiders in the nest begin to disperse; the spherical nest breaks up as into dust, but when the disturbance is at an end the minute Spiders, so small as to be almost invisible, re-assemble and again form their little spherical nursery.

The number of species of Spiders is very great and their habits are very diverse and well worthy of study.

Order II. Phalangida.

The Phalangids (Gk. φἄλάγγιον, a venomous kind of spider) or Harvestmen are in common talk usually classed with Spiders, but they differ from the latter in having no waist, that is to say, the abdomen is not separated from the prosoma by a constriction, and

they breathe entirely by tracheae. They have four long and very slender pairs of legs, which easily break, and their eyes are sometimes elevated above the surface of the head on a tubercle like a look-out tower. The abdomen is distinctly divided into segments.

As a rule these creatures are nocturnal and are usually met with in dark corners or amongst the stalks of hay or grass. Their long

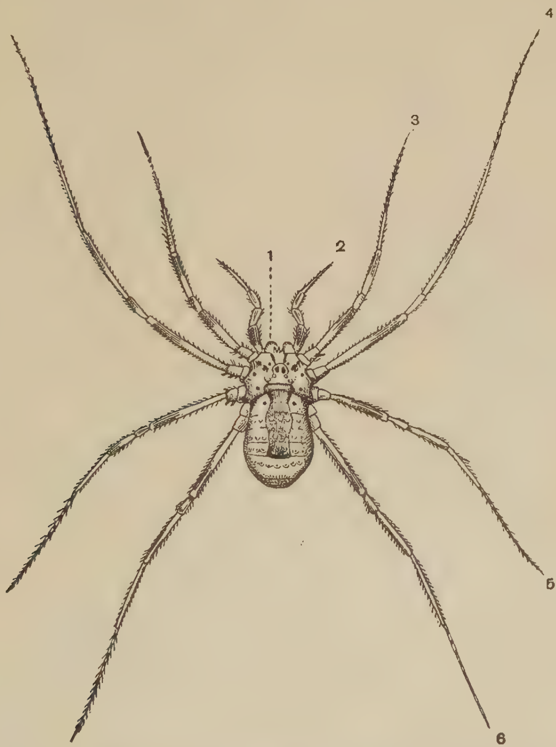

FIG. 120. A Phalangid or Harvestman, *Oligolophus spinosus*, adult male × 2.
1. Chelicerae. 2. Pedipalps. 3, 4, 5 and 6. First, second, third, and fourth legs.

legs enable them to steal with a gliding spring upon their prey, for the most part insects or spiders. They are dull in colour, grey, brown or blackish, as becomes an animal that loves the dusk. About twenty-four species have been recorded in Great Britain. Phalangids die down as winter sets in, but the eggs last through the cold weather and give rise to a new generation in the spring.

Order III. Acarina.

The Acarids (Gk. ἀκἄρές, a morsel) or Mites form an enormous order whose function in life is to a large extent to play the scavenger, and the terrestrial forms confer the same benefits on the dwellers on the Earth that the Ostracoda and many of the smaller Crustacea do on the aquatic fauna. Many of them however have adopted parasitic habits and cause disease amongst larger animals,

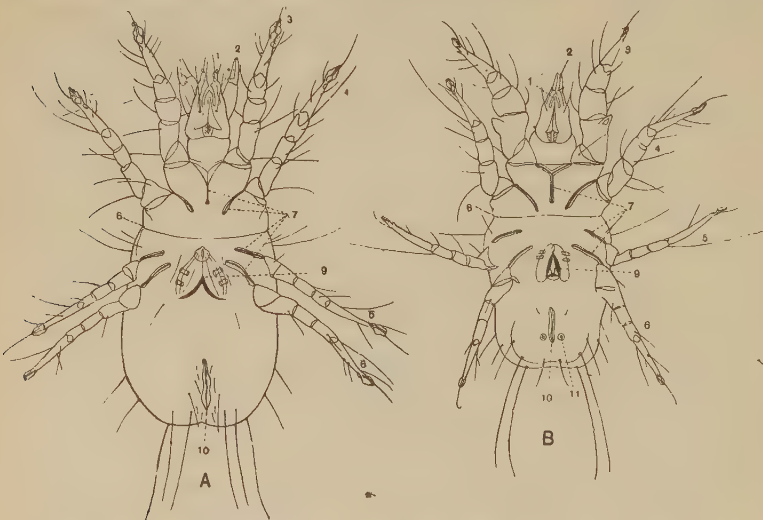

Fig. 121. *Tyroglyphus siro*, seen from the ventral side. A. Female. B. Male. Magnified. From Leuckart and Nitsche.

1. Pedipalpi. 2. Chelicerae. 3, 4, 5, 6. First, second, third and fourth walking legs. 7. Chitinous thickenings supporting legs. 8. Furrow round body. 9. Reproductive opening, flanked by two suckers on each side. 10. Anus. 11. Suckers at side of anus.

while some induce the formation of galls and other deformities amongst plants. Most of the Mites, as their name indicates, are of minute size; but the female Ticks, belonging to the family Ixodidae, which live amongst the undergrowth of forests on the look-out for some vertebrate prey, when they become attached to their hosts —man, cattle, or even snakes—can, by distending their bodies with the blood they suck, swell out to the size of hazel-nuts.

Anatomically Mites are difficult to characterise. Like the Phalangids, they have no waist, and when special breathing organs are present they take the form of tracheae; they differ however from the Phalangids in never showing signs of segmentation. The

chelicerae may be clawed or chelate, like a lobster's claws (Fig. 121), but they often take the form of piercing stylets and the gnathobases of the pedipalpi may form a sheath to protect them.

The number of species is very great; amongst the commoner forms may be mentioned *Tetranychus telarius*, often known as the Red Spider, which spins webs under leaves in which whole colonies shelter. This species is believed to do great damage in hot-houses. *Tyroglyphus siro*, the Cheese-mite, which burrows in decaying cheese, and the genus *Phytoptus*, which causes the conical galls on lime-trees, maples, etc., are also familiar.

Order IV. Scorpionida.

Scorpions are not found in Great Britain, though they are common on the Continent of Europe around the Mediterranean basin and generally in warm climates. They retain a more marked segmentation than is the case with the other Arachnids we have considered. The abdomen is very long, distinctly segmented and differentiated into two portions; (*a*) the mesosoma, consisting of seven segments of the same diameter as the prosoma, bearing the respiratory appendages; (*b*) the metasoma, a much narrower part, consisting of five segments and a curved spine like a tail at the apex of which is the opening of a poison gland. The mesosoma has six pairs of appendages. The first of these forms the genital operculum, a plate bearing on its posterior aspect the genital pore in both sexes; the second are "pectines," curious comb-shaped structures, whose exact function is not yet determined, but which are morphologically reduced and thickened gill-books which project freely and are not enclosed in respiratory chambers. The third, fourth, fifth and sixth segments bear each a pair of lung-books, and it has already been explained that the floors of these are formed of highly modified plate-like appendages which in the adult have lost all trace of their origin from limbs. The seventh segment of the mesosoma shows no traces of limbs and tapers to join the first segment of the metasoma. At the posterior end of the fifth metasomatic segment, on the ventral surface, is situated the anus, and behind this is a conical pointed joint which contains the poison glands and which forms a very efficient and powerful sting. The whole of this tail is very mobile and the sting can readily be directed to any point. In life the tail is usually borne turned forward over the body so that the sting threatens the head.

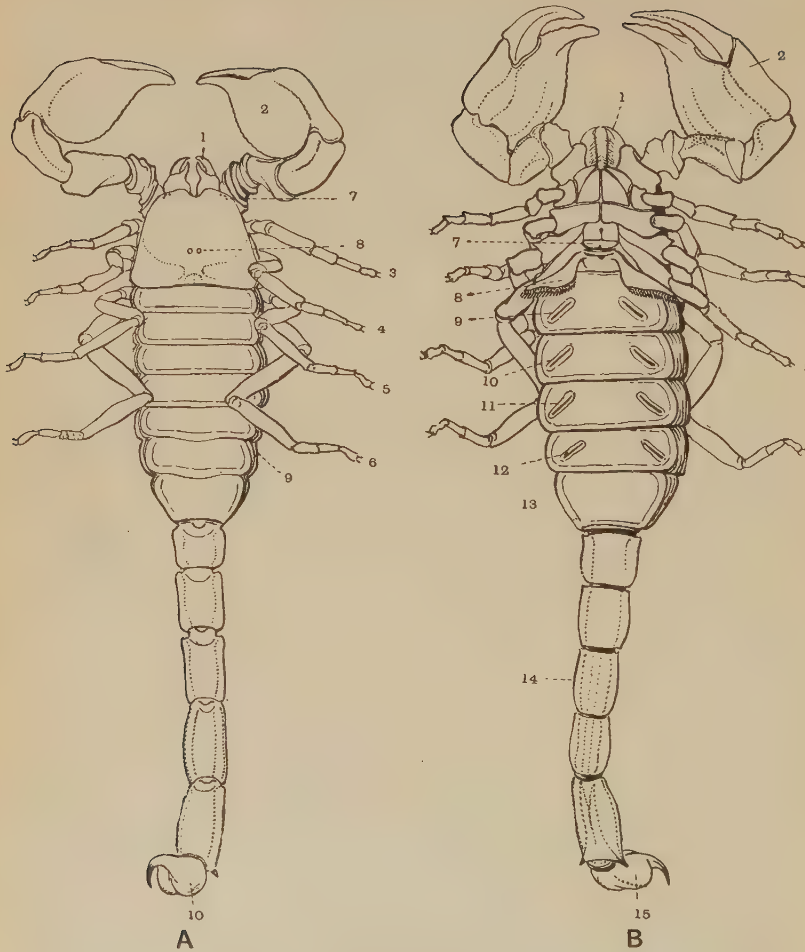

FIG. 122. A. Dorsal view of an Indian scorpion, *Scorpio swammerdami* × $\frac{2}{3}$. B. Ventral view of the same × $\frac{2}{3}$.

A. 1. Chelicera. 2. Pedipalp. 3, 4, 5, 6. 3rd to 6th appendages, or walking legs. 7. Lateral eyes. 8. Median eyes. 9. Soft tissue at side of body, pleura. 10. The poison sting or telson.

B. 1—6 as in A. 7. The genital operculum. 8. The pectines. 9, 10, 11, 12. The four right stigmata leading to the four lung-books. 13. The last segment of the mesosoma. 14. The third segment of metasoma. 15. The telson. In each case the metasoma, which is usually carried bent forward over the meso- and pro-soma, has been straightened out.

Both the chelicerae, which are small and short, and the pedipalpi, which are long and six-jointed, end in nippers, the latter recalling the appearance of the claws of a lobster. The four pairs of walking legs end in claws.

The mouth is very minute, for like the Spiders Scorpions only suck the juices of their prey. They feed for the most part on Insects and Spiders. The basal joints of the first two pairs of

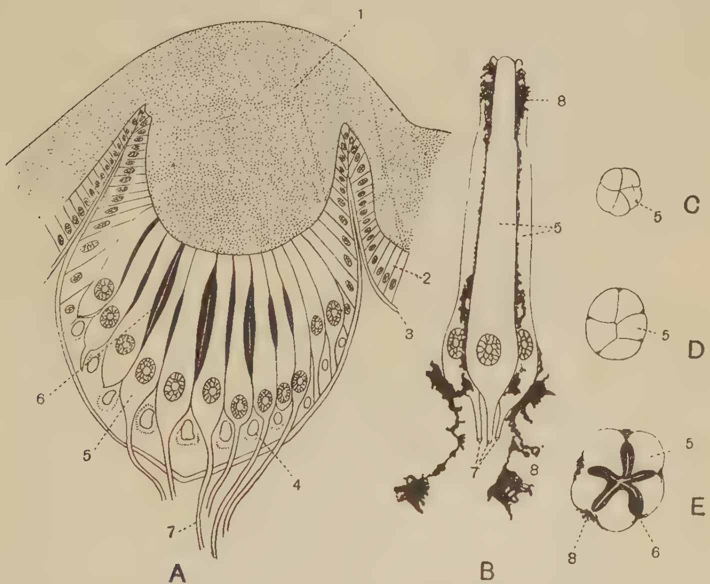

FIG. 123.

A. Vertical section through a lateral eye of a Scorpion, *Euscorpius italicus*. B. Diagram of retinula of a Scorpion's central eye. C, D, E. Transverse section of B taken at different levels. From Lankester and Bourne.

1. Cuticular lens. 2. Epidermis of the general body-surface. 3. Basement membrane. 4. Epidermal cells which contain pigment. 5. Nerve end-cells with nuclei. 6. Rhabdome. 7. Fibres of optic nerve. 8. Pigment contained in connective tissue cells.

appendages, like those of the pedipalps in Spiders, are all produced towards the mouth, forming gnathobases which probably help to hold their food.

The eyes of Scorpions are simpler than those of Spiders and are amongst the simplest type of eye found amongst Arthropoda. As Fig. 123 shows, the lateral eyes are simply shallow pits of the ectoderm. The cells forming one of these pits secrete more cuticle

than the neighbouring ectodermal cells, and this thicker patch of cuticle forms the lens. Some of the pit-cells secrete visual rods on their lateral surfaces. Several of these rods coalesce to form a characteristic rhabdome, or striated spindle characteristic of Arthropodan eyes. The bases of the cells which secrete the rods are prolonged into nerve fibres. The central eyes have a layer of clear cells lying above the visual cells; this is the crystalline layer and acts the part of an additional lens. The visual cells of the central eye are arranged in groups called retinulae, consisting of six or seven cells which surround a central rhabdome.

Scorpions usually hide under rocks and stones during the day, being often very intolerant of heat, but they creep out as dusk comes on and run actively about. The Scorpion is viviparous, the young being born in a condition resembling their parents.

Order V. **Xiphosura.**

A very peculiar aquatic Arachnid called *Limulus*, or popularly the "King-crab," inhabits the warm seas on the Western side of the Pacific Ocean and along the shores of the Western Atlantic. It is a littoral form, that is to say, it lives not far from the shore; it burrows in sand or mud at a depth of from two to six fathoms, often lying with only its eyes, which are on the top of the body, exposed.

The shape of the body is something like a half-sphere with a piece cut out and a long spine is attached to the truncated side. This spine has given the name Xiphosura (Gr. ξίφος, a sword; οὐρά, a tail) to the Order. The half-sphere is hinged, and the part in front of the hinge is the prosoma; the rest is the abdomen, or meso- and meta-soma. On the upper surface of the half-sphere are a pair of simple eyes near the middle line, and there are a pair of compound eyes situated further back nearer the edge. The under surface of the half-sphere is partially hollowed out and concealed in this hollow on each side of the middle line of the prosoma are six pairs of appendages. The most anterior of these are typical nipper-like chelicerae, the next is not specially modified to form a pedipalp, but it and the remaining four pairs are walking legs. All of them send inwards a spiny gnathobase, which helps to form the border of the mouth. The sixth pair of limbs end in some flattened blade-like structures which assist in digging and burrowing in the sand and in extracting the worms which form the principal item of the diet of the King-crab. Behind these limbs are a pair of oval spiny

plates termed the chilaria; these have been proved to be the vanishing limbs of a vestigial segment. This segment appears in the embryos of the Scorpion and the Spider, but is totally suppressed in the adults of these animals. The next appendages,

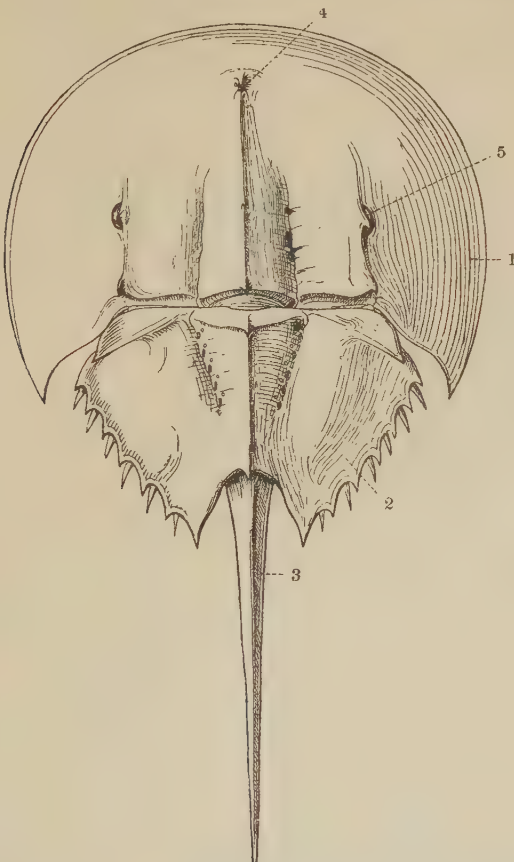

FIG. 124. Dorsal view of the King-crab, *Limulus polyphemus* $\times \frac{1}{2}$.

1. Carapace covering prosoma. 2. Meso- and meta-soma. 3. Telson. 4. Median eye. 5. Lateral eye.

usually reckoned as the seventh, or the first on the mesosoma, take the form of a flattened plate or operculum which bears the reproductive pores on its posterior surface. It is bent back and underlies the eighth, ninth, tenth, eleventh, and twelfth pairs of appendages, which are also plate-like and each of which bears on

its posterior surface a gill-book. There is a striking similarity between these organs and the "lung-books" of the Scorpion; but the gill-books are not sunk in pits. The metasoma terminates at the anus, but behind it a long sword-like tail projects. This

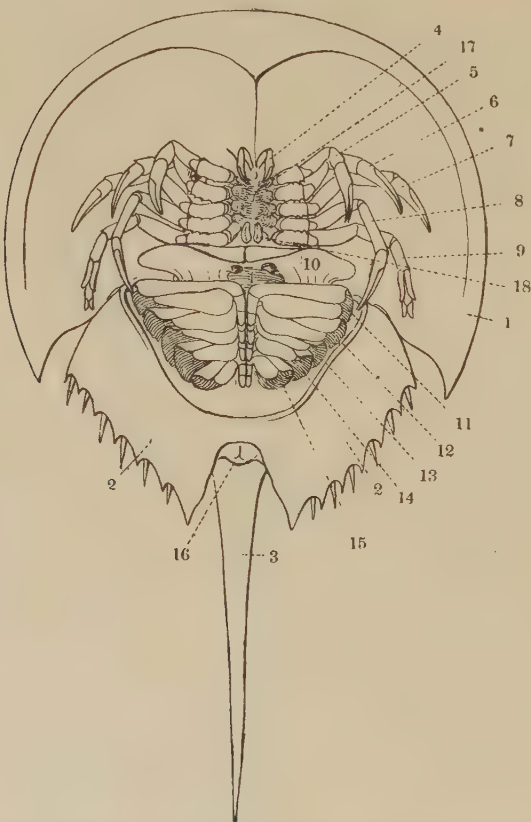

FIG. 125. Ventral view of the King-crab, *Limulus polyphemus* × ½.

1. Carapace covering prosoma. 2. Meso- and meta-soma. 3. Telson. 4. Chelicera. 5. Pedipalp. 6, 7, 8, 9. 3rd to 6th appendages, ambulatory limbs. 10. Genital operculum turned forward to show the genital aperture. 11, 12, 13, 14, 15. Appendages bearing gill-books. 16. Anus. 17. Mouth. 18. Chilaria.

post-anal tail corresponds with the swollen stinging tail or telson of the Scorpion. It is used by the animal to right itself when it is upset by the motion of the waves.

A curious plate of fibro-cartilage to which muscles are attached

lies inside the body near the ventral surface. It is formed of modified connective tissue in which a cheesy material termed chondrin has been deposited in the ground substance, and it is largely built up of interlacing tendons of muscles so that it acts as an internal supporting structure or endoskeleton. It is called the endosternite. Possibly it was a feature of primitive Arthropoda, as similar endosternites occur in many other Arachnida and in some of the more primitive Crustacea.

The internal anatomy differs in many points of detail from that of the Spider, but in essentials there is a fairly close resemblance. Unlike the Scorpion, *Limulus* lays eggs and these are fertilised in the water and pass through what may be termed a larval stage.

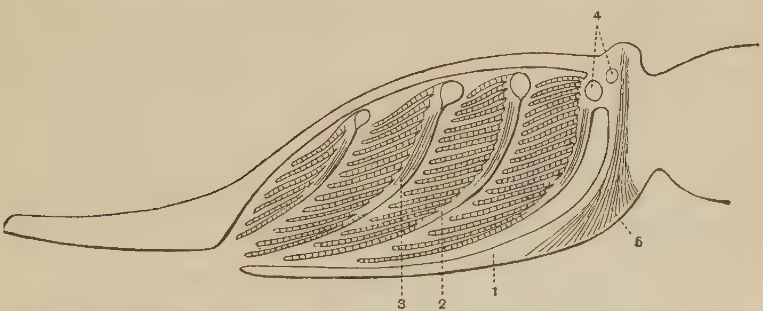

FIG. 126. Section through the operculum and gills of a King-crab, *Limulus*. × about 16. The normal number of gills in a Limulus is five, the section from which this drawing is made showed only four.

1. Operculum. 2. 2nd gill-book. 3. Muscle which moves gills up and down. 4. Blood-vessels. 5. Muscle which raises the operculum.

In many respects Limulus seems to be related to the extinct *Eurypterina*, whose fossil forms are so abundant in the Upper Silurian and Old Red Sandstone formations; and like some species of *Limulus* they attained a great size, two feet or more in length being not uncommon. The Eurypterines were aquatic and indeed seem to form an intermediate stage between the Scorpion and *Limulus*, and confirm us in the conclusion drawn from the anatomy of *Limulus* that this animal retains in many points the habits and structure of the marine ancestors of Arachnida.

The PANTOPODA, familiarly known as Sea-Spiders, are small marine animals about the size of spiders or harvest-men, which are found under the stones at low tides on many parts of our coast. They live on colonies of Hydrozoa and other small sessile animals. They resemble Arachnida in some points and

indeed were formerly classed with them. Like Arachnida, none of their limbs are converted into jaws, indeed none of them have any process which could be called a gnathobase and the first pair, the chelophores, have the form of a little pair of pincers like the chelicerae of Arachnida but are three-jointed not two-jointed like chelicerae. There are also four pairs of long many-jointed legs. But in other points they differ widely from Arachnida. None of the legs are situated in front of the mouth; this opening is found at the end of a snout-like outgrowth of the body called the proboscis. Further, when all the legs are developed as is the case in the genus *Nymphon*, it is found that there are three pairs of reduced legs in front of the first walking leg so that the walking legs cannot exactly correspond in Arachnida and Pantopoda. The third pair of reduced legs are always developed in the male even when absent in the female, and when the female lays the eggs the males attach them to these "ovigerous legs" and carry them about till they are hatched.

There is no abdomen and no tracheae, and the genital organs in many cases have several pairs of ducts opening at the bases of the walking legs. This last feature definitely separates Pantopoda from Arachnida and establishes their right to be regarded as an independent sub-division of Arthropoda.

The TARDIGRADA are minute Arthropoda which live amongst moss and heather; they are of microscopic dimensions. Their cuticle is so thin that we cannot distinguish sclerite and arthrodial membrane. In this they resemble *Peripatus* and they also resemble *Peripatus* in the form of their appendages of which they have only four pairs. These appendages are short stumpy legs each ending in two claws. Perhaps another resemblance to *Peripatus* may be seen in the fact that there is a globular buccal cavity into which two stilet-like lancets project, by which the Tardigrada pierce the cells of the plants on whose juices they live. It will be remembered that in *Peripatus* the single pair of jaws have the form of blades inside a buccal cavity surrounded by a lip. The genital organ opens into the rectum behind and so do two Malpighian tubes. This last feature separates them from *Peripatus*, and if we are not prepared to regard the Tardigrada as minute degraded relatives of that primitive form we must accord them the dignity of an independent class of Arthropoda.

Phylum ARTHROPODA.

Bilaterally symmetrical Coelomata whose coelom has undergone great reduction and has been functionally replaced by the haemocoele. The body is divided into segments which are usually arranged in groups. Paired hollow and jointed limbs on some of the segments.

Class I. Crustacea.

Aquatic Arthropods usually breathing by gills, with two pairs of antennae. At least three pairs of limbs are changed into gnathites.

Sub-class A. Entomostraca.

Small, simple Crustacea with varying number of segments. The appendages behind the gnathites form a uniform series. The stomach has no teeth. The larva is a Nauplius.

Order 1. **Phyllopoda.**

Entomostraca with leaf-like swimming appendages.

Sub-order i. **Anostraca.**

Long-bodied Phyllopoda without carapace, second antennae converted into grasping organs, eyes stalked (5 or 6 pairs), numerous swimming appendages.

Ex. *Branchipus*, *Artemia*.

Sub-order ii. **Notostraca.**

Long-bodied Phyllopoda with flattened horizontally extended carapace vestigial antennae and sessile eyes. Numerous swimming appendages.

Ex. *Apus*.

Sub-order iii. **Conchostraca.**

Phyllopoda with bivalve carapace. Enlarged swimming second antennae with ten or twelve pairs of swimming appendages to which the eggs are attached.

Sub-order iv. **Cladocera.**

Small, short Phyllopoda with bivalve carapace, a dorsal brood-pouch and enlarged swimming second antennae, few swimming appendages.

Ex. *Daphnia*, *Simocephalus*.

Order 2. **Ostracoda.**

Small Entomostraca with unsegmented bodies. At most seven pairs of appendages. Appendages behind the gnathites leg-like and cylindrical. Body completely enclosed within a bivalve carapace.

Sub-order i. **Podocopa.**

With unbranched second antennae and carapace with entire outline.

Ex. *Cypris.*

Sub-order ii. **Myodocopa.**

With forked greatly enlarged second antennae and notched carapace.

Ex. *Cypridina.*

Order 3. **Copepoda.**

Small clearly segmented Entomostraca devoid of carapace with long well developed antennae. Four or five pairs of biramous thoracic appendages.

Ex. *Cyclops.*

Order 4. **Cirripedia.**

Sessile Entomostraca whose body is not clearly segmented and is enclosed in a carapace strengthened by calcareous plates. Usually five biramous thoracic appendages. Hermaphrodite as a rule.

Ex. *Lepas, Balanus.*

Sub-class B. Malacostraca.

Large Crustacea as a rule with twenty segments. The appendages behind the gnathites are differentiated into two series, peraeopods and pleopods—the region to which the latter are attached being termed the abdomen.

Order 1. **Leptostraca.**

Malacostraca with the carapace in the form of a bivalve shell covering the eight free thoracic segments but not fused with them, abdomen of eight segments, the last two of which do not bear limbs. The telson represented by a caudal fork. Thoracic limbs leaf-like.

Ex. *Nebalia.*

Order 2. **Thoracostraca.**

Malacostraca in which the carapace is fused with the thoracic segments and in which the valves of the caudal fork have coalesced to form a telson. Eyes stalked.

Sub-order i. **Schizopoda.**

Thoracostraca with eight pairs of biramous thoracic appendages.

Division i. **Euphausidacea.** [Classed by Calman as Eucarida.]

Schizopoda with ramified liver and carrying the eggs on swimmerets.

Ex. *Euphausia.*

Division ii. **Mysidacea.** [Classed by Calman as Peracarida.]

Schizopoda with single tubular liver and carrying the eggs in a brood chamber protected by oostegites.

Ex. *Mysis.*

Sub-order ii. **Decapoda.** [Eucarida.]

Thoracostraca in which the last five thoracic appendages uniramous and used for walking.

Division *a.* **Macrura.**

Abdomen long.

Ex. *Astacus.*

Division *b.* **Anomura.**

Abdomen of moderate length, last one or two pairs of thoracic legs short and inserted higher up on the side of the body than the rest.

Ex. *Pagurus.*

Division *c.* **Brachyura.**

Abdomen short, devoid of tail fin.

Ex. *Cancer, Carcinus.*

Sub-order iii. **Stomatopoda.** [Hoplocarida.]

Thoracostraca in which the carapace is reduced in length leaving the last thoracic segments free. The first five pairs of thoracic appendages developed into grasping organs called "maxillipedes." Abdomen large and bearing gills on its appendages.

Ex. *Squilla.*

Sub-order iv. **Cumacea.** [Classed by Calman as Peracarida.]

Thoracostraca in which the carapace is reduced leaving four or five thoracic segments free. Two pairs of true maxillipedes. Eyes fused into one immovable almost sessile eye.

Ex. *Cuma, Diastylis.*

Order 3. **Arthrostraca.** [Peracarida.]

Malacostraca in which the carapace is absent. One or rarely two thoracic segments fused with the head, the rest free. Eyes sessile.

Sub-order i. **Amphipoda.**

Body laterally compressed. Gills on thoracic appendages.

Ex. *Gammarus.*

Sub-order ii. **Isopoda.**

Body dorso-ventrally compressed. The endopodites of some of the abdominal appendages are soft and vascular and act as gills.

Ex. *Asellus, Porcellio, Oniscus.*

Sub-order iii. **Tanaidacea.**

Body uncompressed, abdominal appendages unmodified, two thoracic segments fused with the head, a vestigial carapace sheltering one gill.

Order 4. **Syncarida.**

Malacostraca in which the carapace is completely absent but in which the eyes are stalked. The thoracic limbs carry swimming exopodites and branched epipodites.

Ex. *Anaspides.*

Class II. Antennata.

Arthropoda with a single pair of antennae and with tracheal respiration.

Sub-class A. Prototracheata. [Onychophora.]

Soft, caterpillar-like Antennata with numerous pairs of appendages. Numerous pairs of coelomiducts acting as excretory organs.

Ex. *Peripatus.*

Sub-class B. Myriapoda.

Antennata, with a head bearing two pairs of jaws well marked off from body, which consists of many similar segments bearing six- or seven-jointed appendages. Excretory organs are ectodermal. Malpighian tubules.

Order 1. **Chilopoda.** [Opisthogoneata.]

Myriapoda flattened dorso-ventrally, bases of legs wide apart: to each tergum corresponds one pair of legs: the segment following the head has a large pair of poison claws: genital opening between the last pair of legs.

Ex. *Lithobius.*

Order 2. **Diplopoda.** [Progoneata.]

Cylindrical Myriapoda with the bases of legs close together: to each tergum behind the fourth correspond two pairs of legs: no poison claws: genital opening on the third segment behind the head.

Ex. *Iulus.*

Sub-class C. Insecta.

Antennata with the body divided into three regions, head, thorax and abdomen. Head bears the antennae and three pairs of persistent mouth parts; thorax three pairs of walking appendages and usually two pairs of wings; abdomen as a rule without appendages, genital opening on one of the posterior segments of the abdomen.

Order 1. **Aptera.**

Wingless insects with hairy and scaly bodies ending in anal filaments. No metamorphosis.

Ex. *Lepisma.*

Order 2. **Orthoptera.**

Jaws biting, fore- and hind-wings usually unlike. Metamorphosis incomplete.

Ex. *Forficula*, *Stylopyga*, *Phasma*, *Acridium*, *Gryllus.*

Order 3. **Paraneuroptera.**

Jaws biting. Wings alike, membranous, with many nervures. Metamorphosis incomplete. Larvae aquatic with rectal respiration.

Ex. *Aeschna.*

Order 4. **Ephemeroptera.**

Jaws vestigial in adult. Wings alike, membranous, with many nervures. Metamorphosis incomplete. Larvae aquatic, breathing by tracheal gills.

Ex. *Ephemera.*

Order 5. **Isoptera.**

Jaws biting. Wings alike, membranous, with many nervures. Metamorphosis incomplete. Larvae subterranean. A social system with castes of workers and soldiers.

Ex. *Calotermes*, *Eutermes.*

Order 6. **Thysanoptera.**

Jaws stabbing and sucking. Wings alike, small, fringed with hairs. Metamorphosis with pupal stage and therefore complete.

Ex. *Thrips.*

Order 7. **Trichoptera.**

Jaws sucking only. Wings alike, covered with hairs. Metamorphosis complete. Larvae aquatic, with tracheal gills, and living in tubes.

Ex. *Phryganea.*

Order 8. **Neuroptera.**

Jaws biting. Wings alike, membranous, with many nervures. Metamorphosis complete.

Ex. *Siales*, *Myrmeleo*, *Hemerobius*, *Chrysopa.*

Order 9. **Coleoptera.**

Jaws biting. Anterior wings hard and meeting each other with a median, straight suture. Metamorphosis complete.

Ex. *Coccinella*, *Melolontha.*

Order 10. **Hymenoptera.**

Jaws biting and licking. Four membranous wings with few nervures. Metamorphosis complete.

Ex. *Formica*, *Apis*, *Vespa.*

Order 11. **Hemiptera.**

Jaws piercing and sucking. Wings alike or different. Metamorphosis incomplete.

Ex. *Acanthia*, *Cicada*, *Aphis.*

Order 12. **Diptera.**

Jaws piercing and sucking. Hind-wings reduced, front-wings membranous. Metamorphosis complete.

Ex. *Culex*, *Musca.*

Order 13. **Siphonaptera.**

Jaws piercing and sucking, but differently constructed from those of Diptera. Wings absent. Metamorphosis complete.

Ex. *Pulex.*

Order 14. **Lepidoptera.**

Jaws sucking. Four similar wings covered with scales. Metamorphosis complete.

Ex. *Bombyx.*

Class III. Arachnida.

Arthropoda with no antennae and no true gnathites. Prosoma of six appendage-bearing segments followed by an abdomen (occasionally divided into mesosoma and metasoma) whose appendages when present are usually plate-like.

Order 1. **Araneida.**

Abdomen soft, unsegmented. Four to six spinnerets, two to four lung-books and in the former case two tracheae.

Ex. *Epeira.*

Order 2. **Phalangida.**

No waist between prosoma and abdomen, the latter region segmented. Tracheae, no lung-books.

Ex. *Oligolophus.*

Order 3. **Acarina.**

No waist. Abdomen unsegmented. Tracheae, no lung-books.

Ex. *Tyroglyphus, Tetranychus.*

Order 4. **Scorpionida.**

Abdomen divided into a mesosoma of seven segments and a metasoma of five segments and ending in a post-anal poisonous telson. Four pairs of lung-books.

Ex. *Scorpio.*

Order 5. **Xiphosura.**

Prosoma of shield-shaped outline with a broad margin. Abdomen unsegmented. Gill-books. The telson forms a spine.

Ex. *Limulus.*

Class IV. Pantopoda.

No gnathites and no masticatory processes of any kind attached to the appendages. All the appendages leg-like. No tracheae. Several pairs of genital apertures.

Ex. *Nymphon.*

Class V. Tardigrada.

Cuticle thin, no distinct sclerites, gnathites a pair of stilets within the buccal cavity. Only four other pairs of appendages and these are stumpy legs ending in claws.

CHAPTER XIII

PHYLUM MOLLUSCA

Mollusca (Lat. *mollis*, soft) is the name which is given to one of the largest and most important phyla of the animal kingdom. In it are included not only our terrestrial snails and slugs and many fresh-water species but also the oysters, mussels, periwinkles, whelks and countless other species of "shell-fish," bivalve and univalve, which crowd the rocks laid bare at low-water around our coasts: and in addition to these, the extraordinary Octopuses, Squids and other forms of Cuttle-fish belong to the same great phylum. The name Mollusca seems to have been suggested by the fact that the members of the phylum do not possess any internal hard parts such as are found in Man and other vertebrates. This softness of internal constitution is shared by other classes with no relation to the Mollusca, as for instance the great group of the Arthropoda. The Arthropods however possess a horny covering which closely invests them and follows every irregularity of their outlines, so that it seems a real part of themselves. This is the exoskeleton or cuticle, which constitutes one of the great differences between them and the Mollusca. The latter, it is true, possess also an exoskeleton composed principally of calcareous matter, but this adheres only to a part of the surface. It is usually very thick and easily detached, and so it is frequently looked on as a separate thing from the animal and is known as the shell. The shell is to be looked on as a secretion produced by a part of the skin only: this part of the skin, which almost always projects from the rest of the body as a flap, is called the mantle. The space between the mantle-flap and the rest of the body is known as the mantle-cavity. The mantle-cavity shelters the gills or organs of respiration, and into it open the kidney or kidneys and the anus, and usually also the genital ducts.

General description.

Class I. Gastropoda.

In order to fix our ideas we may take the common English garden snail, *Helix aspersa*, which has also established itself throughout considerable areas in North America, or, if procurable, the larger *Helix pomatia*, which on account of its size

Description of Snail.

is easier to dissect, as a type of the Mollusca. In Lower Canada the genus *Helix* is not very abundant, and the largest species, *Helix albolabrus*, is rather small for convenient dissection. *Limnaea stagnalis*, the large river-snail, is however common and easy to obtain, and its structure is similar in its main outlines to that of *Helix*.

The shell is coiled into a spiral form; the body contained in it consists of a visceral hump, coiled like the shell and closely adhering to it, and of a portion which we call the head, neck, and foot, which can be drawn within the opening of the shell if the animal is alarmed, but which under ordinary circumstances is quite outside it. The snail is devoid of anything in the nature of legs,—an important character of the Mollusca as contrasted with the Arthropoda,—but

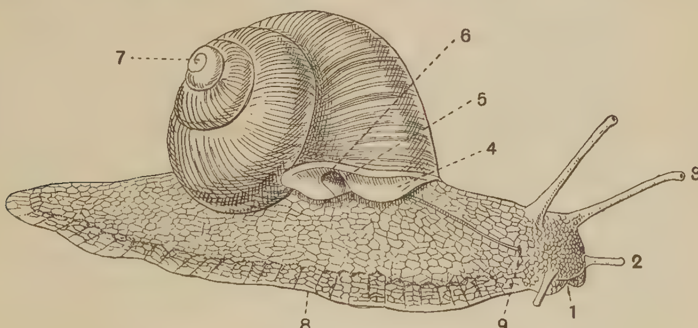

FIG. 127. *Helix pomatia.* Side view of shell and animal expanded. From Hatschek and Cori.

1. Mouth. 2. Anterior tentacles. 3. Eye tentacles. 4. Edge of mantle 5. Respiratory pore. 6. Anus. 7. Apex of shell. 8. Foot. 9. Reproductive aperture.

the part of the body next the ground is a flat muscular surface called the foot. By means of wave-like contractions of the muscular fibres of this organ the snail moves along, always preparing the ground for itself by depositing a layer of slime on it. This slime is poured forth from a gland which opens in front of the foot, just beneath the mouth (14, Fig. 130). The foot is one of the most important organs of the Mollusca; it takes different shapes in the different groups but always assists locomotion. In the pond-mussel, for instance, it is shaped like a wedge, in order to force a path through the soft mud at the bottom of the ponds in which the animal lives. The different shapes which the foot assumes afford the chief basis for the classification of Mollusca. The motion of the foot has been analysed by Prof. Parker. The wave-like contractions which pass backwards over

the surface of the foot are contractions of the vertical (dorso-ventral) muscles connecting the foot with the body—as each part of the foot in succession is lifted from the substratum the transverse fibres contract and by forcing forward the blood cause this part to lengthen and move forwards. Then as the wave passes this part acquires a new adhesion to the substratum, the longitudinal muscles then contract and pull the rest of the foot after the extended part.

The head of the snail bears two pairs of feelers, or tentacles, which are hollow outgrowths of the body-wall (2, 3, Fig. 127): these when irritated are protected by being pulled outside in, and so are brought into the interior of the body. The first or shorter pair are supposed to be the chief seat of the sense of smell: the second and longer pair have at their tip a small pair of black eyes. These eyes are merely minute sacs, the walls of which are made of light-perceiving cells, connected at their bases with a nerve which leads to the brain; in the cavity of the vesicle is a horny lens which nearly fills it up. The eyes of nearly all the Mollusca are constructed on the same plan, but in the Cuttle-fish not only is the vesicle large and spacious and the lens proportionately smaller, but there is in addition a series of folds of skin surrounding the place where the eye comes to the surface, which constitute an outer chamber, and outside this, eyelids, so that the whole organ acquires a superficial similarity to the human eye.

If we carefully pick away the shell of the animal and lay bare the visceral hump, brushing away any mucus which may adhere to the body, we shall see on the right side of the animal a round hole (5, Fig. 127). A bristle passed through this reaches into a large cavity separated from the outside by an exceedingly thin wall. This space is nothing but the mantle-cavity, which, as explained above, is the space comprised between the projecting mantle flap and the rest of the body. The peculiarity about the snail is that the mantle edge has become fused to the back of the neck so as to shut the mantle-cavity off from the exterior, leaving only this little hole of communication. The mantle-cavities of the marine allies of the snail, such as the whelk and periwinkle, are not so completely shut off, inasmuch as in them the mantle flap merely lies against the neck but is not fused to it, and inside the mantle-cavity there is a gill. This gill consists of a hollow axis bearing on one or both sides a close set row of thin plates inside which the blood circulates and receives oxygen from the water by diffusion. Fresh supplies of water are drawn into the mantle-cavity by the action of myriads of

cilia which cover the gill. A gill of this nature is called a ctenidium, owing to its comb-like appearance (Gr. κτενίδιον, a small comb). Now, since the snail breathes air, not water, it has lost the gill, but to compensate for the loss it has changed the whole mantle-cavity into a lung. The floor of the mantle-cavity, really the back of the neck, is arched and composed of muscles : when these contract the floor flattens and thus the mantle-cavity is enlarged and air is drawn in.

The blood is contained in large vessels running in the thin roof of the mantle-cavity : these are clearly seen when the mantle flap is clipped away from the neck and turned over to the right (8, Fig. 128, and Fig 129). These vessels are seen to all converge to the heart, which consists of two small oval sacs placed end to end. That into which the vein enters is thin-walled and is called the auricle: the other thicker one is called the ventricle (Fig. 129); it is the more muscular of the two and drives the blood through two arteries to the body. One of these passes up to the visceral hump, and the other forward to the head and neck. In Molluscs which have gills the auricle always receives the blood from the gill : when there is one gill, as is the case with nearly all the univalves, there is only one auricle: but where, as in the bivalves and cuttle-fish, there are two or even four gills (as in *Nautilus*) there are likewise two or four auricles. The heart is surrounded by a space called the pericardium, which really corresponds to the body-cavity or coelom of Vertebrates, Annelids and Echinoderms,

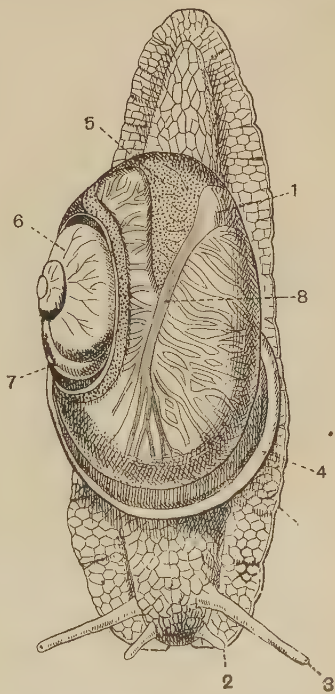

FIG. 128. *Helix pomatia*. The animal seen from the dorsal side after removal of the shell. From Hatschek and Cori.

1. Auricle of the heart receiving pulmonary vein. 2. Anterior tentacles. 3. Eye tentacles. 4. Edge of mantle. 5. Kidney. 6. Liver. 7. Albumen gland. 8. Pulmonary vein. 9. Foot.

for into it the excretory organ opens and in the embryo the genital cells are budded from its wall. Other large spaces existing in the head and neck have no connection with the coelom but are really parts of the blood system. Since there are no regular veins, except those which run in the mantle-roof, the arteries open into irregular spaces. It will be remembered that the space called pericardium amongst the Arthropods is really a blood space and that the heart opens into it by openings called ostia: the coelomic character of the pericardium of Mollusca is then another distinguishing feature of the group. It opens by a narrow ciliated passage, the reno-pericardial canal, into the kidney, which is seen in the mantle-roof beside the pericardium (5, Fig. 128). The kidney looks like a solid yellow organ; but in reality it is a vesicle into the cavity of which numerous folds project, covered by the peculiar cells which have the power of extracting waste products from the blood, which flows in spaces in the kidney wall. The kidney communicates with the exterior by a narrow thin-walled tube, the ureter, which runs along the right side of the body and opens on the lip of the respiratory opening, just above the opening of the anus (10, Fig. 131).

Internal structure.

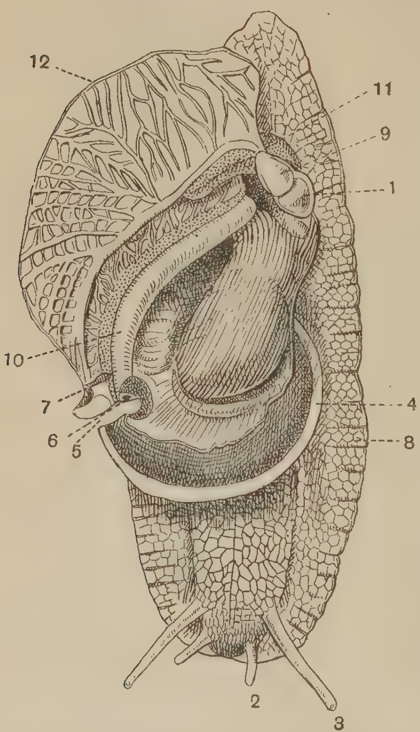

FIG. 129. *Helix pomatia*, with the upper wall of the pulmonary chamber cut open and folded back. From Hatschek and Cori.

1. Ventricle. 2. Anterior tentacles. 3. Eye tentacles. 4. Cut edge of mantle. 5. Respiratory pore. 6. Anus. 7. Opening of ureter. 8. Foot. 9. Auricle receiving pulmonary vein. 10. Rectum. 11. Kidney. 12. Upper wall of pulmonary chamber.

The kidney in Mollusca varies a good deal in structure, but is always built on the same fundamental

plan as that of the snail. Where there are two gills there are likewise two kidneys. Often there is no ureter, but the kidney opens directly to the exterior, as in the Cuttle-fish, the Whelk (*Buccinum*), and the Limpet (*Patella*). In the Cuttle-fish instead of irregular spaces there are regular veins in the walls of the kidney and the special excretory cells are only developed over the course of these veins.

Turning now to the digestive system of the snail we notice several very interesting peculiarities. The mouth is situated in front, beneath the small pair of tentacles, and there is a curved horny bar, the jaw, in the roof of the mouth. Against the jaw works a rasp-like tongue, called the radula, the surface of which

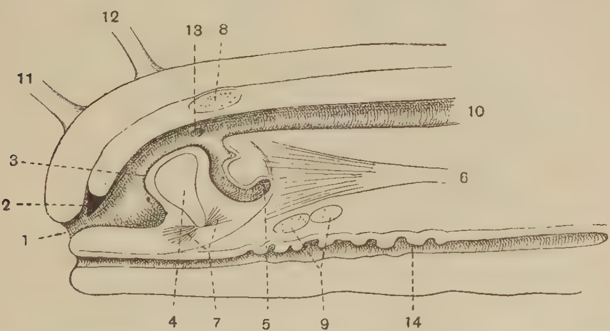

FIG. 130. Inner view of right half of head of *Helix*, to show the arrangement of the radula × 2.

1. Mouth. 2. Horny jaw. 3. Radula. 4. Cartilaginous piece supporting radula. 5. Radula sac from which radula grows. 6. Muscle which retracts the buccal mass. 7. Intrinsic muscles which rotate the radula. 8. Cerebral ganglion. 9. Pedal and visceral ganglia. 10. Oesophagus. 11. Anterior tentacle. 12. Eye tentacle. 13. Orifice of duct of salivary gland. 14. Mucous gland which runs along foot and opens just under the mouth.

is a horny membrane covered with myriads of minute, recurved teeth. Underneath this membrane there are certain small pieces of cartilage to which muscles are attached which pull the cartilages and the membrane covering them alternately downwards and forwards and upwards and backwards, so that the tongue is worked against the jaw. Thus the snail is enabled to tear pieces out of the leaves on which it feeds (Fig. 130). A similar organ is found in all Mollusca, except the bivalves or Lamellibranchiata, and the number, shape and arrangement of the teeth are an important help in classification. The horny membrane is continued backward into

a little blind pouch, called the radula sac: here is its growing-point, where new teeth are continually being formed as the old ones wear away. In the Limpet (*Patella*), this radula sac is extra-

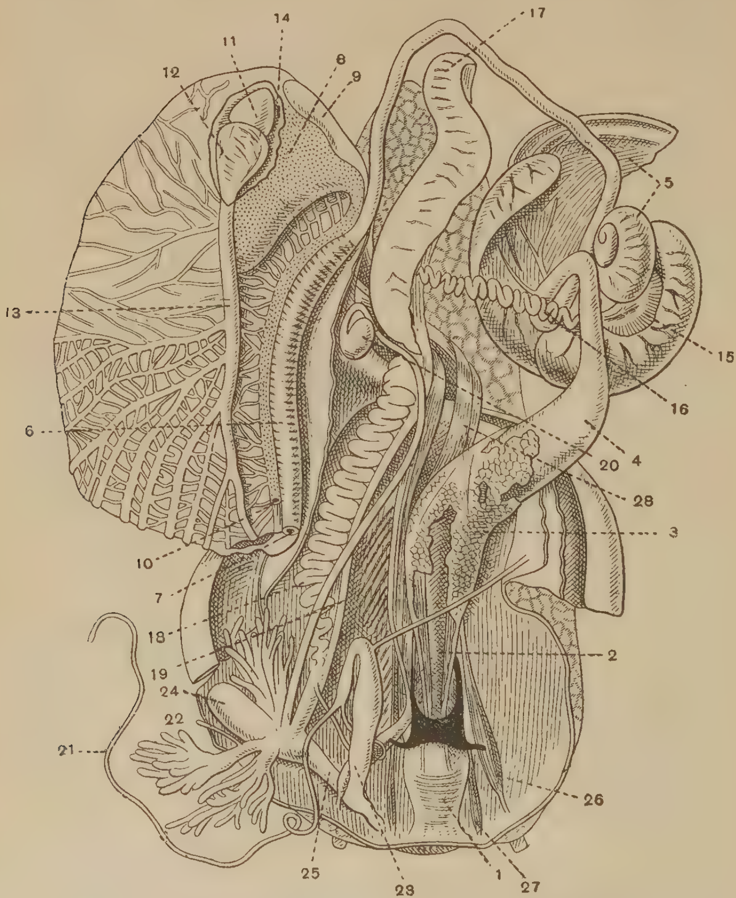

FIG. 131. *Helix pomatia*, opened and the viscera exposed. From Hatschek and Cori.

1. Pharynx. 2. Oesophagus. 3. Salivary glands, with duct. 4. Stomach. 5. Liver. 6. Rectum. 7. Anus. 8. Kidney. 9. Inflated commencement of ureter. 10. Opening of ureter to exterior. 11. Ventricle. 12. Auricle. 13. Pulmonary vein. 14. Opening of kidney into pericardium. 15. Ovo-testis. 16. Common duct of ovo-testis. 17. Albumen gland. 18. Female duct. 19. Male duct. 20. Spermatheca. 21. Flagellum. 22. Accessory glands. 23. Penis. 24. Dart sac. 25. Vagina. 26. Eye tentacle, retracted. 27. Anterior tentacle, retracted. 28. Muscles which retract the head, pharynx, tentacle, etc.

ordinarily long, attaining a length two or three times greater than that of the body. In the Cuttle-fish the radula is present and the jaw is developed into upper and lower beaks, like those of a parrot, with which the animal tears its prey to pieces. The bivalves have lost all trace of both jaws and radula: they live on the microscopic organisms brought to them in the currents of water which they produce, and so they do not need to masticate their food.

The radula sac and the muscles and cartilages belonging to the radula, form a swelling which is called the buccal mass. Behind this comes the oesophagus or gullet, which appears narrow by comparison, but its cavity is really as large as the space inside the buccal mass. The gullet soon widens out into the first stomach or crop, which is used for storing the food. On the outside or surface of this two branching whitish structures are seen, the salivary glands. They secrete a juice which runs forwards through two tubes, the salivary ducts, opening into the buccal mass. The saliva mingles with the food as it is being masticated. The crop is situated in the hinder part of the neck, and behind it the alimentary canal passes under the mantle-cavity and up into the visceral hump. The great mass of this hump is occupied by a brownish looking organ, called the liver. This, like the similarly named organ in the Arthropoda, is a great mass of tubes lined by cells of a deep brown colour: the tubes join together and eventually open by two main tubes, one above and one below, into a dilatation of the alimentary canal. This swelling is the true digestive stomach. It is probable that the "liver" assists digestion by preparing a fluid which is poured into the stomach: its function is thus not the same as that of the human liver. In fact it must be confessed that the name liver has been recklessly given by the older naturalists to any brown-coloured organ found near the stomach of an Invertebrate. The part of the alimentary canal behind the true stomach is called the intestine. It takes a turn in the liver substance and then runs out of the visceral hump along the right side of the body to open by the anus, which, as we have seen, is placed just behind the respiratory opening.

The central nervous system resembles that of the Annelida in being made up of ganglia, each of which might be compared to a miniature brain, connected together by means of commissures, that is, bands of nerve fibres. The two largest ganglia, which are placed above the oesophagus one at each side and connected by a commissure, are called the supra-oesophageal or cerebral ganglia,

or sometimes the brain (1, Fig. 132); but there is no reason to think that they are any more important to the animal than the others. Underneath the oesophagus there is what at first sight seems to be a compact nervous mass, connected with the supra-oesophageal ganglia by a commissure on each side forming a nerve collar (Fig. 132). Closer inspection shows that this mass is perforated by a hole through which passes the great anterior artery from the ventricle, and that from both the lower and upper halves a separate nerve comes off to go to the cerebral ganglia. Thus the apparently simple nerve collar consists of two commissures on each side united in a common sheath. Between them a minute nerve passes down, to end finally in a minute membranous sac lined by ciliated cells and cells with sense hairs and containing fluid in which a little ball of carbonate of lime floats. This sac, the otocyst, is the only other important sense-organ, besides the eyes, which the snail possesses. It is difficult to dissect, but if the small bivalve *Cyclas* be taken, the shell opened and the foot cut off and slightly compressed, or if one of the transparent Molluscs, such as *Pterotrachea*, which float on the surface of the sea, be examined, it is perfectly easy to see both otocysts with the microscope. It used to be supposed that the function of this organ was to perceive sound, but whilst it is probable that some vibrations of the air affect it, it is nearly certain that, like the otocysts of Medusae and Arthropoda, its main function is to enable the Mollusc to keep its balance by allowing it to perceive whether it is leaning on one side or not. As the snail changes its position the little ball inside rolls about and affects different parts of the wall of the vesicle, and hence probably different fibres in the nerve which supplies it.

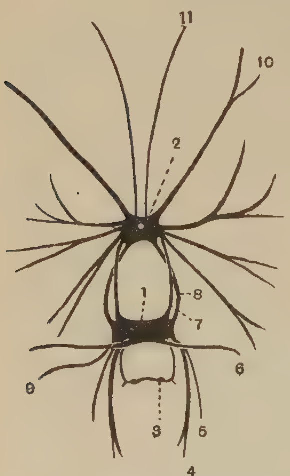

FIG. 132. View of nervous system of *Helix pomatia*.

1. Cerebral ganglion. 2. Pedal, pleural, and visceral ganglia. 3. Buccal ganglia. 4. Nerve to lips. 5. Olfactory nerve. 6. Optic nerve. 7. Pleuro-cerebral commissure. 8. Pedo-cerebral commissure. 9. Genital nerve. 10. Nerve to mantle. 11. Nerve to viscera.

Not all Mollusca possess eyes, but all, except perhaps the Oyster, which never moves, possess otocysts. The experiment of

cutting them out has been made in the Cuttle-fish, and it is then found that the animal loses its power of keeping its balance in the water and tumbles about.

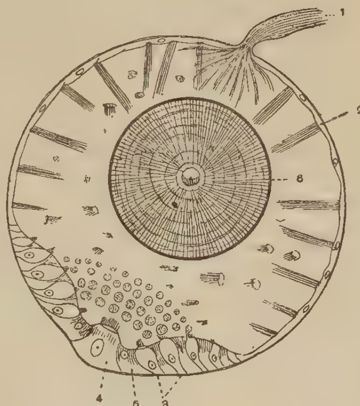

Fig. 133. Optical section through the auditory vesicle or ear of *Pterotrachea friederici*, a transparent pelagic Mollusc × about 150. After Claus.

1. Auditory nerve. 2. Ciliated cells. 3. Auditory cells. 4. Large central auditory cell. 5. Supporting cells. 6. Otolith.

To return to the central nervous system. In the pond snail, *Limnaea*, the hinder part of the sub-oesophageal nervous masses consists of no less than five ganglia, strung together on a short loop of nervous fibres, which is called the visceral loop. Of these a pair nearest the head are called the pleural ganglia, the next are called the visceral ganglia, and the one at the end the abdominal ganglion (Fig. 134). The front and lower part of the sub-oesophageal nervous mass consists of the pedal ganglia, which send nerves exclusively to the foot. Pleural and visceral ganglia can be recognised in the young snail, but they become indistinguishably joined in the adult. In other Molluscs, such as the Sea-hare (*Aplysia*), or the Ear-shell (*Haliotis*), the visceral loop is long and the ganglia widely separated. In these animals it can be seen that the pleural ganglia send nerves to the sides of the body, and that from the visceral ganglia nerves come off which go to the base of the gill or gills. At the base of each gill

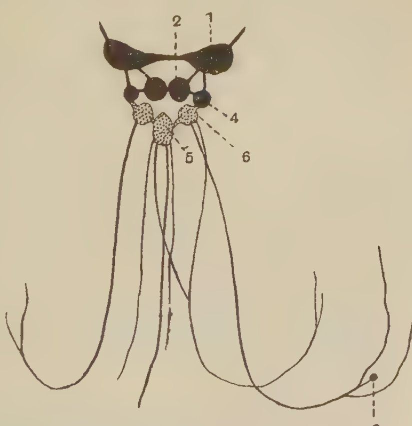

Fig. 134. Nervous system of *Limnaea*. After Lucaze-Duthiers.

1. Cerebral ganglion. 2. Pedal ganglion. 3. Osphradial ganglion. 4. Pleural ganglion. 5. Abdominal ganglion. 6. Visceral ganglion.

there is a patch of thickened skin, called an osphradium (Gr. *ὀσφραίνομαι*, to smell), provided with numerous sense-cells, which enables the animal to test the water which enters its mantle-cavity. Of course no such organ exists in the snail. The muscles of the radula are supplied by nerves from a special pair of small ganglia placed on the buccal mass—the buccal ganglia—connected with the supra-oesophageal ganglia.

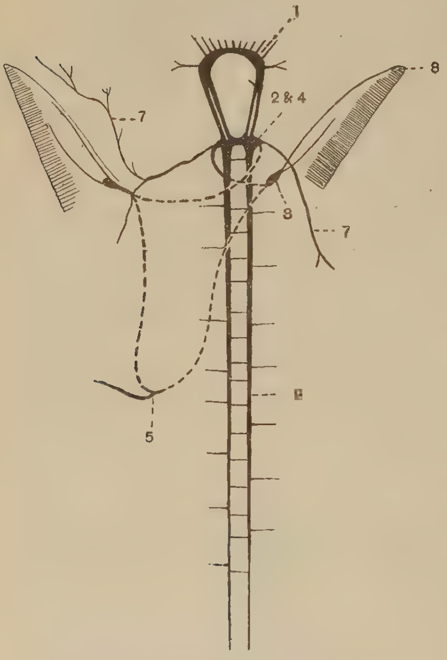

FIG. 135. Nervous system, osphradium (olfactory organ) and gills of *Haliotis*. After Lacaze-Duthiers.

1. Cerebral ganglion. 2. Pedal ganglion. 3. Osphradial ganglion. 4. Pleural ganglion. 5. Abdominal ganglion. 7. Nerves to mantle. 8. Gills. 9. Pedal nerves.

We thus see that the nervous system of the snail consists of a pair of supra-oesophageal ganglia connected by commissures with (*a*) a pair of pedal ganglia supplying the muscles of the foot with nerves, (*b*) an extremely short visceral loop, the ganglia on which are so closely placed as to become practically confluent with each other, whence nerves go to all parts of the body, and (*c*) a small pair of buccal ganglia supplying the buccal mass. The nervous systems of all Mollusca are built on this plan: in the bivalves, however, where there is no radula, not only are the buccal ganglia absent, but the pleural and cerebral are fused with one another, and, as the visceral loop is long, we find three widely separated pairs of ganglia,—cerebro-pleural, pedal, and visceral—the last named often termed "parieto-splanchnic," in different parts of the body. The Cuttle-fish have a closely massed nervous system like the snail, which is protected in a kind of rudimentary skull, made of cartilage.

The only organs of the snail which remain to be mentioned are the reproductive organs. These are exceedingly complicated in this Mollusc, both sexes being united in the same individual, a condition of affairs which is known as hermaphroditism. The essential genital organ is the ovotestis, a small yellowish patch of delicate tubes spread out on the surface of the liver, on the inner side of the uppermost coil of the spire (Fig. 131). This organ produces both eggs and spermatozoa and both travel down a single tube. Before the duct reaches the neck it receives the secretion of a large organ, called the albumen gland. This secretion consists of a fluid which has proteids in solution and is of high nourishing value. Beyond the albumen gland although externally simple the duct is divided by a septum into two passages, one for the eggs and one for the spermatozoa, and still further on it becomes completely divided into two separate tubes. The female portion opens to the exterior by a thick-walled muscular part, the vagina, into which a tuft of tubes—the mucous glands—opens. The vagina also receives the opening of an organ called the spermatheca, which is a round sac at the end of a long duct in which the spermatozoa received from another individual are stored up. In addition to this, a thick-walled sac called the dart-sac also communicates with the vagina. In this sac is found a calcareous rod which is thrown out into the body of another individual about the time of fertilisation. The male duct also opens into a muscular organ called the penis, which can be partly everted, that is, turned inside out, and so protruded. The function of this organ is to transfer the spermatozoa to another individual; it has a blind pouch projecting inward beyond the place where the male duct enters it called the flagellum: in this the spermatozoa are massed together into bundles called spermatophores. Both penis and vagina have a common genital opening far forward on the right side of the neck (Fig. 127).

Few Mollusca have such complicated generative organs as the snail. One large group of marine snails, the Opisthobranchiata, resemble *Helix* in being hermaphrodite, but none possess the dart-sac, and in many the generative opening is placed further back and connected with the opening of the penis by a groove called the seminal groove. Hence the penis is obviously derived from a muscular pit on the side of the head into which the spermatozoa trickled and was at first unconnected with the generative opening.

In another group of marine snails, the Prosobranchiata, there is

a separation of the sexes and the albumen gland is absent. The penis in these Mollusca is not a sac which can be turned inside out, but a projecting lobe of the body, often of great size. In the most primitive Mollusca—the Solenogastres—the genital organ remains throughout life a thickening of the wall of the pericardium or coelom; the eggs and spermatozoa drop into the pericardium and find their way out by coelomiducts, just as is the case with Annelida.

This is the case also in Cephalopods, where, however, there were originally four kidneys, and the one or two which serve as generative ducts are specialised for this purpose; thus the duct is in the male prolonged into a papilla which serves as the penis. A commoner case is for the generative organ to be closely connected with one kidney and to burst directly into it. This is found in the simpler Prosobranchiata, such as the Limpet (*Patella*), the Ear-shell (*Haliotis*) and their allies. In *Nucula* and the simplest bivalves there are two generative organs and they open into both kidneys; in the Pond-mussels (*Anodonta* and *Unio*), and all more modified forms, they open independently close to the kidney openings. There is little doubt that in all Mollusca the tube conveying away the generative products was originally a kidney or a part of one.

Asymmetry of body.

Having got some idea of the arrangement of the organs of the snail we must proceed to consider certain points about the form of the body considered as a whole. If we except the genital opening, the head and neck of the snail are exactly bilaterally symmetrical in their outer form; on each side there is a taste-tentacle and an eye-tentacle and the mouth and the opening of the mucous gland are exactly in the middle line. Most of the ordinary animals we see—birds, quadrupeds, fishes, insects, worms, etc.—are bilaterally symmetrical with regard to external appearance and many with regard to internal organs also. The peculiarity of the snail is that, while it follows the ordinary rule as far as the head, neck and foot are concerned, it departs from it with respect to the visceral hump and the included organs. The shell is, as we all know, spiral, but this shape is due to the shape of the visceral hump contained within it, by the activity of the skin of which the shell is produced. This spiral shape again is simply due to one side being longer than the other, and it is connected with the shortness of the right side that we find the opening of the anus on the right side. In all bilaterally symmetrical animals this opening is situated in the middle line, but in some of the marine

allies of the snail—the Whelk, Limpet and others forming the group Prosobranchiata—the inequality of the two sides of the visceral hump is carried to such an extent that the anus is brought right round so as to open nearly over the middle of the neck; and where, as in the Ear-shell (*Haliotis*), there are two gills, the left becomes pushed over to the right side and the gill belonging to the right side becomes displaced to the left and both gills come to be in front of the heart. Since the visceral ganglia are connected with the bases of the gills, one side of the visceral loop becomes pulled over the other in consequence of the displacement of the gills (Fig. 135). This condition of the nervous system is called the streptoneurous condition; it exists in one division of the Molluscs which are ordinarily termed "sea-snails." Such Mollusca with a twisted loop are termed Prosobranchiata (Gr. πρώσον, in front), and though most of these have only one gill, the twisting of the visceral loop may be regarded as a proof that they originally had two. In the other large division of the sea-snails, the Opisthobranchiata (Gr. ὄπισθεν, behind), the shell is generally small or has quite disappeared, and since where this has taken place there seems to have been a tendency to undo the twisting, the anus becomes pushed back to nearly the posterior end of the body and the visceral loop becomes straightened out and shortened. The gill when present is behind the heart. There is reason to believe that this last process has gone on in the snail, though it has kept its shell. It appears then that the curious spiral form of part of the body and the inequality of the sides have something to do with the possession of a large shell by a crawling animal. We do not understand very clearly how the one thing has brought about the other, but we can understand that there would be a tendency in a tall visceral hump to topple over to the one side or the other and thus exercise a greater strain on one side than on the other and the side which was stretched would tend to grow faster than the other. If we start therefore with a simple cap-like shell with a round opening and if this shell grows as we know it does by the prolongation of the lips of the opening and if the lip grows faster on one side than on the other a spiral shell must result. Certain it is, at any rate, that the only existing Mollusca which possess large coiled shells and yet are bilaterally symmetrical, are the pearly *Nautilus* and another rare Cuttle-fish (*Spirula*), which do not crawl but swim.

The class or primary division of the Mollusca to which the snail belongs is called the Gastropoda, on account of the flat smooth

foot or crawling surface which they all possess (Gr. γαστὴρ, the belly; ποῦς, ποδὸς, foot). The shell is typically composed of a single piece, never of paired pieces; and from this circumstance is derived the general term "univalve" often applied to the Gastropoda by collectors; in one small division of the class (the Isopleura) however the shell is represented by eight pieces placed one behind the other in the middle line.

Class II. Lamellibranchiata = Pelecypoda.

Fresh-water Mussel. The characters mentioned at the end of the last section sharply separate the Gastropoda from another class of Mollusca, the Lamellibranchiata or Pelecypoda, to which the common mussel and innumerable marine

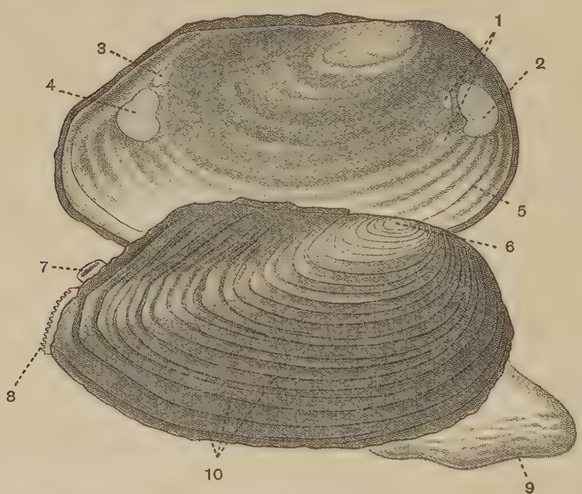

Fig. 136. Shell containing *Anodonta mutabilis*, and behind it the inner face of an empty left shell.

1 Points of insertion of the anterior retractor (above) and of the protractor muscles (below) of the foot. 2. Point of insertion of the anterior adductor muscle. 3. Point of insertion of the posterior retractor of the foot. 4. Point of insertion of the posterior adductor muscle. 5. Lines formed by successive attachments of the mantle. 6. Umbo. 7. Dorsal siphon. 8. Ventral siphon. 9. Foot protruded. 10. Lines of growth.

forms, such as the Oyster, Clam, Cockle, etc., belong. The Molluscs belonging to this class have a shell composed of two similar pieces, the right and left valves, united by a horny flexible piece, the hinge (Fig. 136). The foot is typically formed like a wedge or axe-head

whence the name Pelecypoda (Gr. πέλεκυς, a hatchet), and is used as a plough to force a way through the mud in which the creatures live. There are many species of pond- or river-mussels in North America: *Anodonta cygnaea* is perhaps the commonest in England, but in places *Unio pictorum* is abundant; *A. cygnaea* occurs in Canada and the United States and in these countries *Unio complanatus* is also common. Any one of these forms will serve our purpose. The shell is about four inches long and two inches high, and is covered with a black horny layer, the so-called periostracum. The shell is apt in places to be eroded by the action of the carbonic acid in the water. Underneath it is a thick slightly translucent layer of crystals of carbonate of lime, called the prismatic layer. The inner part next the mantle is composed of thin layers placed one above the other. This is the mother-of-pearl or nacreous layer, which in many Molluscs has an iridescent sheen, owing to its action on light. These three layers are also present in the shell of the snail and in all other Molluscan shells, but they are very easily made out in the shell of the pond-mussel. To the periostracum the colour of the Molluscan shell is mainly due. The periostracum and prismatic layers are formed by the edge of the mantle and if destroyed they cannot be replaced. The nacreous layer is deposited by the whole surface of the mantle. If by chance a grain of sand gets wedged in between the mantle and the shell it is apt to become covered with layers of mother-of-pearl, and in this way a pearl-like blister is formed. The more costly pearls however arise within the soft parts of the body, and appear to consist of concentric layers of nacreous substance surrounding some parasitic larva and secreted by the mollusc as a defence against the attacks of the parasite. The shell is marked by a series of curved lines running parallel to one another. These lines mark the limits of growth attained in each year, the amount intervening between two lines being the amount of growth accomplished in a year. It will be seen that the common focus around which the curves run is not in the centre of the hinge line, but decidedly nearer one—the anterior—end. This common focus is called the umbo, and it represents the shell with which the *Unio* started life (6, Fig. 136).

The Shell.

As might be expected from the shape of the shell, the mantle has the form of two great flaps hanging down at the sides of the body. The flaps have a free edge in front, below and behind, but pass into the general wall of the body, with which they fuse, above.

The edges of the mantle flaps are very much thickened and closely adherent to the shell; as stated above, it is by these edges alone that the periostracum and the prismatic layer are formed.

The hinge is strictly speaking part of the shell; it is secreted by the ectoderm of the back of the animal between the two mantle lobes. When the valves of the shell are pressed closely together the hinge is bent out of shape and by its elasticity it tends to throw the valves apart; hence when a mussel is dead the valves always gape.

The two valves in *Unio* articulate with one another by means of teeth. There are a pair of stout teeth a little in front of the

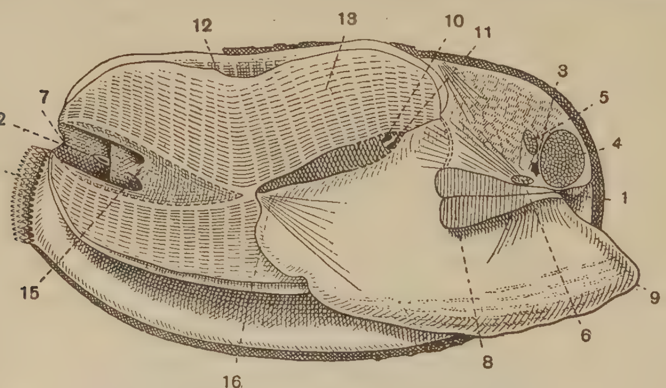

FIG. 137. Right side of *Anodonta mutabilis* with the mantle cut away and the right gills folded back × about 1. From Hatschek and Cori.

1. Mouth. 2. Anus. 3. Cerebro-pleural ganglion. 4. Anterior adductor muscle. 5. Anterior retractor muscle of the foot. 6. Protractor muscle. 7. Dorsal siphon. 8. Inner labial palp. 9. Foot. 10. External opening of kidney or organ of Bojanus. 11. Opening of genital duct. 12. Outer right gill-plate. 13. Inner right gill-plate. 14. Ventral siphon. 15. Epibranchial chamber, the inner lamellae of the right and left inner gills having been slit apart. 16. Posterior protractor muscle.

umbo, on the left valve, working on either side of one tooth on the right valve; these are called the cardinal teeth. A long ridge on the right valve, working between two ridges on the left valve, is called the lateral tooth. *Anodonta* derives its name (Gr. ἀν-, not; ὀδούς, ὀδόντος, a tooth) from the circumstance that the shell is devoid of teeth.

When the shell is removed from the animal the cut ends of the fibres of two large muscles are seen. These muscles, which run transversely from the one valve to the other, are called the anterior and posterior adductors respectively,

The Body.

and it is by means of them that, when danger threatens, the animal closes the valves and shelters foot, gills and body, within. Just behind the anterior adductor is a pair of small muscles running into the foot, and these are the anterior retractors of the foot. A similar pair, the posterior retractors, are found just in front of the posterior adductor, and by the combined action of the four retractors the shell is drawn forward, the foot being (relatively) fixed

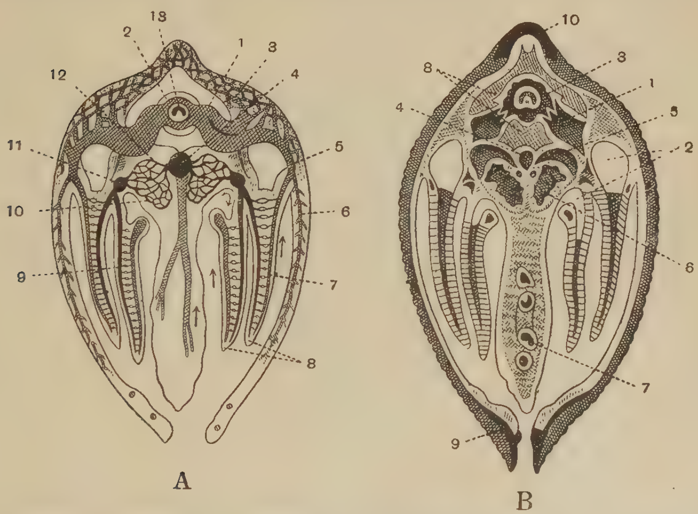

FIG. 138. A. Diagrammatic section through *Anodonta* to show the circulation of the blood. B. Section through *Anodonta* near the posterior edge of the foot. From Howes.

A. 1. Right auricle. 2. Ventricle. 3. Keber's organ. 4. Vena cava. 5. Efferent branchial trunk. 6. Efferent pallial vessel. 7. Efferent branchial vessel. 8. Branchiae. 9. Afferent branchial vessel. 10. Efferent renal vessel. 11. Afferent branchial trunk. 12. Afferent renal vessel. 13. Rectum.

B. 1. Right auricle. 2. Epibranchial chamber. 3. Ventricle. 4. Vena cava. 5. Non-glandular part of the kidney. 6. Glandular part of the kidney. 7. Intestine in foot. 8. Pericardium. 9. Shell. 10. Ligament of shell.

in the mud (Figs. 137, 140). The foot is thrust forth by the forcing of blood into it, through the contraction of the muscles which underlie the skin in various parts of the body. The protractors (of the foot) enable the animal to move backwards when necessary. They are a pair of muscles inserted in the shell below the anterior adductor and their fibres proceed upwards to join the upper part of the foot. A small group of muscles running from the mantle to

be attached to the shell near the umbo pull the shell downward and help to plough a furrow in the mud. The animal moves by forcing out the foot and wedging it in the mud in front and then drawing the body after it.

At the sides of the body on each side we find the branchia or gill, or ctenidium, which as in the Gastropoda consists of a hollow axis bearing two rows of plates. The ctenidium is, however, highly modified in *Unio*. The axis is attached high up to the side of the body in front but projects freely into the mantle cavity behind. The plates have become narrowed so as to form long filaments, and the ends of each row are bent up and are, in the case of the outer row, fused to the mantle lobe. The bent-up ends of the inner row are joined to the foot in front and to the corresponding parts of the ctenidium of the other side behind, but in the middle they are free, at least in some species (Fig. 138). Successive filaments of one row are welded together into a plate, called a lamella, by the fusion of their adjacent edges, leaving only occasional holes for the percolation of the water, so that individual filaments appear like ridges on a ploughed field (Figs. 137, 139). The descending and bent-up ends of the same filament are tied together by cords or narrow plates of tissue traversing the space between them. These cords and plates are called interlamellar junctions, since they unite two lamellae. The pieces of tissue uniting the filaments are called interfilamentar junctions, or collectively, subfilamentar tissue. Gill-plate is the name given to the whole mass composed of one row of V-shaped filaments: there is thus an outer and an inner gill-plate on each side, and each gill-plate has two lamellae formed from the descending and ascending limbs of the filaments, respectively (Fig. 138). It is this peculiar modification of the ctenidia which has suggested the name Lamellibranchiata for the class.

Each V-shaped filament is clothed on its outside, that is, the side looking away from the concavity of the V, with high ectoderm cells carrying powerful cilia; these are of two kinds, and from their respective positions are termed frontal and lateral cilia respectively. By the latter a strong current of water is produced entering between the posterior borders of the mantle lobes, which normally gape slightly. On this current the animal depends both for respiration and nutrition, since the food consists entirely of the minute animals and plants swept in with the water. The normal position of the Mussel is to have the anterior end deeply embedded in the sand or mud and the posterior end protruding; the animal

moves only when for some cause the water becomes unsuitable for its purposes.

Since the upturned ends of the inner rows of filaments of both ctenidia are united behind the foot, a bridge is formed dividing the mantle cavity into an upper or epibranchial and a lower or hypobranchial division. The gaping opening between the mantle lobes at the posterior end is similarly divided into an upper portion, the dorsal siphon, and a lower, the ventral siphon. Since it is the

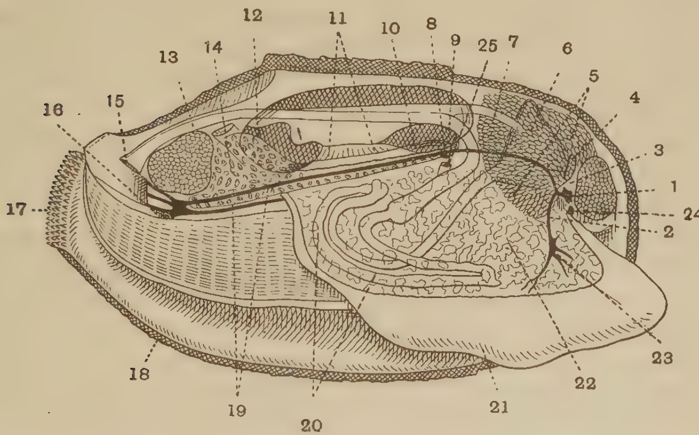

FIG. 139. Right side of *Anodonta mutabilis*, dissected to show the viscera × about 1. From Hatschek and Cori.

1. Cerebro-pleural ganglion. 2. Cerebro-pedal commissure. 3. Oesophagus. 4. Anterior protractor muscle. 5. Liver. 6. Stomach. 7. Aorta. 8. External opening of organ of Bojanus or kidney. 9. Internal opening of the same. 10. Pericardium. 11. Right auricle. 12. Posterior end of ventricle passing into posterior aorta. 13. Rectum. 14. Glandular part of kidney. 15. Anus. 16. Opening of epibranchial chamber. 17. Ventral siphon. 18. Edge of shell. 19. Cerebro-visceral commissure. 20. Intestine. 21. Foot. 22. Reproductive organs. 23. Pedal ganglion of right side. 24. Mouth. 25. Opening of the reproductive organ.

outer lower surfaces of the filaments which are clothed with cilia, it is into the ventral siphon and hypobranchial chamber that the current passes. The lips of both siphons—especially the ventral siphon—are plentifully beset with small papillae, which are sensitive to light and shade. If the shadow of the hand be allowed to pass over them the mantle edges are instantly drawn together and the siphons thus closed. In the Scallop (*Pecten*) similar papillae are developed into well-formed eyes. Part of the water passes through

the small holes left between the gill-filaments and so into the epibranchial chamber and escapes by the dorsal siphon, carrying with it the matter cast out from the kidneys and the anus. As this water percolates through the gills the blood which circulates in these organs receives oxygen from it and gets rid of carbonic acid.

In front of the gills there are situated two organs called labial palps, on each side of the anterior part of the animal (8, Fig. 132). These are triangular flaps, an upper and lower on each side, the surfaces of which are covered with grooves clothed with abundant cilia on the sides turned towards one another. The two superior labial palps are connected by a narrow ridge crossing above the mouth; the two inferior labial palps by a similar ridge beneath it. The mouth thus lies at the bottom of a trough,—the lips of which are formed by the superior and inferior labial palps respectively. The mouth is situated beneath the great anterior adductor muscle which projects beyond it like a forehead. Not all the cilia on the grooves crossing the labial palps however serve to convey food to the mouth; some on the contrary serve to remove excess of food from the mouth. It has been shown that on each ridge separating two grooves the cilia on the posterior surface beat towards the mouth but those on the opposite side away from the mouth. As in the natural position the ridges tend to incline and overlap each other towards the mouth the cilia which are effective are those which drive food to the mouth. When the animal has had enough or the food is distasteful a nervous impulse causes blood to be forced into the ridges; they are erected and then the repulsive cilia remove the unused food from the mouth. This food would decay and form a breeding ground for harmful germs if it were not got rid of. Food is conveyed to the mouth by a band of short cilia borne by the strip of ectoderm running along the lower edge of the inner gill-plate where the descending and ascending limbs of the filaments pass into each other. The so-called "frontal cilia" which clothe the outer sides of the ascending and descending limbs of the filaments of the inner gill-plate produce currents which flow downwards towards this mid ventral strip of ectoderm and wash towards it all particles which are too large to pass through the gill-pores. The ventral strip of ectoderm contains not only ciliated cells but also glandular cells which produce mucus. In this secretion the minute organisms contained in the water are ensnared and the whole cord of mucus thus produced is worked forwards towards the mouth at the anterior edge of the gill-plate where it falls on to the palps and is by them taken to the mouth. The rejected food is transferred from the

palps to a band of ciliated ectoderm running along the inner side of the mantle lobe near its edge until it reaches the ventral siphon when it is ejected. The current produced by the frontal cilia covering the outer lamella of the outer gill-plate passes upwards to join a current produced by cilia on the mantle: that produced by the frontal cilia covering the inner lamella of the outer gill-plate passes upwards to join the downward current on the outer lamella of the inner gill-plate. The current on the mantle curves round to join the current bearing away the rejected food, but if the palps are swollen out so as to touch the mantle, the food conveyed by this current passes to them and can be utilised by the mouth.

The alimentary canal shows a considerable resemblance to that of the snail. No trace, however, of radula, buccal mass, crop or salivary glands, is to be seen. A short oesophagus leads at once into the stomach, which is a wide sac receiving right and left the ducts of the two lobes of the liver. The intestine runs vertically down into the foot, makes several loops there and then turns back and reaches nearly to the point from which it started, i.e., the hinder end of the stomach. Thence it pursues a straight course through the pericardium and over the posterior adductor muscle, to end in an anal papilla which projects into the epibranchial mantle-cavity. The cavity of the first part of the intestine after it leaves the stomach is invaded by two opposite folds termed the major and minor typhlosoles which almost divide it in two viz. a narrow groove on the right and a cylindrical space on the left. The former, termed the intestinal groove, serves to convey undigested matter to the anus the latter, termed the style-sac, secretes a clear gelatinous rod called the crystalline style. This rod is kept in constant rotation by cilia and is worked forward towards the stomach. Where its front end touches the stomach wall this forms a cuticular structure called the gastric shield. The front end is constantly melting away: and as the rod contains a digestive ferment it has been called solid gastric secretion. The rod is not found in specimens which have been deprived of food for some time such as those commonly used for dissection in the class-room. The straight concluding portion of the intestine is called the rectum. The pericardium is situated in the mid-dorsal line posterior to the stomach. The fact that it surrounds the rectum is the consequence of its origin in the embryo as a pair of sacs lying to the right and left of the intestine, which later meet above and below this organ.

There are, as mentioned above, two kidneys formerly called "nephridia" in the mussel. These, frequently termed the organs

of Bojanus, are dark coloured bodies situated beneath the floor of the pericardium on either side of the vena cava. Each consists of a U-shaped tube lying horizontally, with one limb placed vertically above the other and the bend directed backwards. The deeper limb is the active part; it has numerous folds projecting into it which are covered with dark cells. It opens into the pericardium in front by a curved slit lined with powerful cilia which produce an outward current. This of course is the reno-pericardial duct such as has been already described in the snail. The outer and upper limb is wide and smooth-walled and opens into the deeper limb beneath the posterior adductor. In front it opens to the exterior through a pore with thick lips placed just above the place where the upturned ends of the inner row of filaments are attached to the foot (Fig. 139).

The kidney, since it is a tube lined with excretory cells and communicating internally with the body-cavity, has been compared with the nephridium of *Lumbricus*, but it is developed as an outgrowth from the coelom not as an ingrowth from the ectoderm like the nephridium of *Lumbricus*. It must rather be compared to the coelomiduct of that worm which serves as genital duct. The function of the internal opening is to convey to the exterior the fluid in the body-cavity, which contains excretory matter thrown out by the cells lining the coelom. The anterior end of the pericardium of the mussel has a brownish red colour and is produced into numerous little pockets lined by peculiar cells, which are excretory in function (Fig. 138). This portion of the pericardial wall is called Keber's organ, and the excreta thrown out by it pass down the reno-pericardial canal.

The heart consists of a ventricle which surrounds the rectum, and two flat triangular auricles, the broad bases of which are inserted into the wall of the pericardium just over the place where the bent-up ends of the outer filaments of the ctenidium are attached to the mantle. From the ventricle blood is driven forwards by an anterior aorta dorsal to the rectum, and backwards by a posterior aorta ventral to the rectum. From these arteries it finds its way into a multitude of irregular spaces in the foot and the other portions of the body, and eventually reaches a vessel, called the vena cava, lying under the floor of the pericardium in the middle line, between the right and left upper limbs of the two kidneys. From the vena cava the blood streams out through many channels in the wall of the kidney and reaches the axis of the ctenidium, whence it makes its way into the filaments. especially those of the outer

row. From the upturned edges of these last it reaches the mantle and from this the auricle. Some blood is sent to the lobes of the mantle, as in the snail, and through the thin skin absorbs oxygen; this blood is returned direct to the auricle without passing through the gill; from this fact it appears that the mantle lobe as well as the gill is a respiratory organ.

In the nervous system the cerebral and pleural ganglia on each side are generally regarded as coalesced, but in *Nucula* a distinct pleural ganglion has been observed on the cerebro-visceral commissure anterior to the pericardium. There is a long visceral loop, ending in two closely conjoined visceral ganglia, placed beneath the posterior adductor (Fig. 139). On either side of these, just where the axis of the ctenidium becomes free from the body, is a thickened patch of yellow ectoderm —the osphradium. This is a peculiar sense-organ, the function of which, it is believed, is to test the water passing over the gill as to suitability for respiration. There are a pair of large otocysts in the foot.

Mussels are male and female: their reproductive organs are paired, and consist on each side of a bunch of tubes spreading through the foot. The ducts are continuous with the walls of the ovary or of the testis. They open by slit-like orifices just in front of the opening of the nephridia on each side of the foot. The spermatozoa are swept out by the water passing through the dorsal siphon and are sucked in by the inhalant currents of female individuals. The eggs when cast out are detained between the two

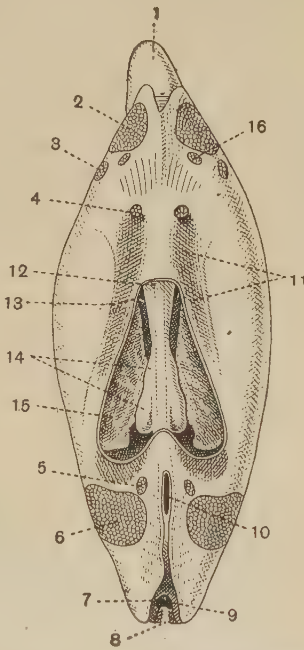

FIG. 140. Dorsal view of *Anodonta mutabilis*, with the upper wall of the pericardium removed to show the heart × about 1. After Hatschek and Cori.

1. Foot. 2. Anterior adductor muscle. 3. Protractor muscle. 4. Depressor muscles. 5. Posterior retractor muscle. 6. Posterior adductor muscle. 7. Dorsal siphon. 8. Ventral siphon. 9. Anus. 10. Split between left and right mantle lobes through which larvae at times leave the epibranchial chamber. 11. Keber's organ. 12. Rectum traversing ventricle. 13. Internal opening of organ of Bojanus. 14. Ventricle. 15. Left auricle. 16. Anterior retractor muscle.

lamellae of the outer gill-plate and there fertilised. They develop into peculiar larvae called Glochidia, provided with a sticky thread or byssus. A bivalve shell is developed but not the foot. When a fish passes by the mother expels the Glochidia from the gills, and they seize hold of the tail or fins of the fish and embed themselves therein. They develop there for some weeks and change gradually into the adult form. They show a remarkable sensitiveness to the presence of fish, but if they fail to attach themselves to one they fall to the bottom of the water and perish.

Lamellibranchiata as a group have very uniform habits: the principal points in which they differ from one another are (1) the degree of complexity which that all-important organ the ctenidium has attained, and (2) the extent to which the animal is able to burrow.

The simplest forms, such as *Nucula*, have ctenidia like those of a Gastropod, a fact which suggests the view now generally held, that the Lamellibranchs are descended from some primitive type of Gastropod.

In others, such as the Sea-mussel (*Mytilus*), the ctenidia have the same external appearance as those of *Anodonta*, but the filaments are very loosely united with one another; they adhere to one another in fact merely by the interlocking of lateral bunches of cilia and their upturned ends are not fused to the mantle. The foot is small and tongue-shaped, the animal never burrows and seldom moves, being fixed by a cord of mucus called the byssus, secreted by a gland in the hinder part of the foot.

In the Oyster (*Ostrea*) the foot has disappeared and the animal passes its life resting on one side. In the Scallop (*Pecten*) the foot has also atrophied, but the animal is able to swim through the water by flapping the valves of the shell. The Cockle (*Cardium*) has a large and powerful foot by which it is enabled to execute leaps.

Mya (sometimes known as the Clam, though this term is applied to many Bivalves) and its allies burrow deeply in the sand and have the edges of the mantle behind drawn out into two long tubes closely apposed to one another, termed the dorsal and ventral siphons. By means of these tubes they keep up a connection with the surface, so that the currents of water are not interrupted. Similar tubular funnels, though not so much drawn out, are seen in the Razor-shell (*Solen*) (Fig. 141). *Pholas* and some others are able to burrow in rock; this is said in some cases to be effected by an acid secretion poured out by the flat disc-like end of the cylindrical foot. *Teredo*, the ship-worm, burrows in timber; the siphons are very long and covered with a shelly deposit; the original valves of the

shell are very small compared with this secondary shelly tube. This animal is very destructive to submerged wooden structures; a wooden pile supporting a pier in Vancouver was reduced to a mere sponge work in the space of eighteen months by the ravages of this Mollusc. The burrowing in this case is effected by the rasping action of the anterior margins of the valves of the shell.

Before we proceed to discuss the highest class of Mollusca which includes the Squids and Cuttlefish, there are two small groups which we must mention, since they cannot be classed either as Gastropoda or as Lamellibranchiata. These are the Solenogastres and the Scaphopoda.

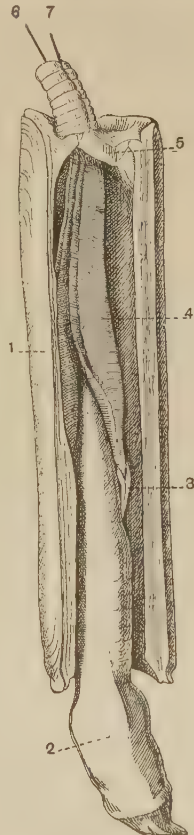

FIG. 141. *Solen vagina*, the Razor-shell, the shell is opened and the posterior part of the mantle is torn to admit of this.

1. Shell. 2. Foot. 3. Labial palps. 4. Gills. 5. Torn portion of mantle. 6. Bristle in ventral siphon. 7. Bristle in dorsal siphon.

Class III. The Solenogastres.

These are small animals confined to the sea and usually found in rather deep water which look at first sight like worms and have nothing in their appearance to suggest that they are allied to Mollusca. When we come to examine their anatomy we find however that they possess an unmistakable radula sac with a radula bearing teeth inside it. Further, many of them possess two comblike gills—i.e. ctenidia—projecting from the hinder end of the body near the anus. They are bilaterally symmetrical animals, and they do not possess a shell, unless the isolated spiclues, secreted by the ectoderm cells of some species, may be regarded as the forerunner of this. The mantle however is represented by a cup-like fold surrounding the anus. There is a pericardium, in the roof of which the heart appears as a ridge projecting downwards. This pericardium is connected with the exterior by two curved tubes which serve both as excretory organs and genital ducts, for the

genital organ is a median mass of cells attached to the front wall of the pericardium and bursts into the pericardium when it is ripe.

The Solenogastres have no foot, but in place thereof there is in most of the genera belonging to this group a median ventral groove clothed with thick cilia in which there is a very slight median ciliated elevation which has been regarded as the first rudiment of a foot. It is to be surmised that the animals use these cilia to glide over the mud in which they live. This groove though absent in the genus *Chaetoderma* has given the name to the group, for Solenogastres means "grooved-bellies" (Gr. σωλήν, a groove). It is one of the most interesting discoveries of the science of Embryology that the more primitive Mollusca and Annelida have in their life history a type of larva called the Trochophore which is almost identical in the two groups and which is regarded by many zoologists as an indication that both groups are descended from a common ancestral form which in some respects resembled the Trochophore. Now in many forms of Trochophore larva there is a ventral ciliated groove and it may be surmised that the Solenogastres diverged from the common ancestral stock of Mollusca very soon after this stock had become distinguishable from the Annelida. The genus *Neomenia* has been dredged in the Firth of Clyde.

Class IV. Scaphopoda.

The members of this group comprise a few species referable to two or three closely allied genera. The name, which means "spade-footed" (Gr. σκάφος, a spade), is unfortunate because although the foot is used for burrowing into the mud in which the animals live there it nothing distinctive about this, for most Pelecypoda (Lamellibranchiata) also possess a foot which is used for burrowing into mud. The foot of Scaphopoda is a cylindrical organ which has a trilobed termination. The lateral lobes of this are capable of being spread out horizontally and so give the foot, when it is driven in, a firm hold on the mud.

The distinctive characteristics of the Scaphopoda are to be found in the mantle and the shell. The latter is tubular and curved, shaped something like an elephant's tusk, it is open at both ends, but the larger opening is the one through which foot and tentacles are protruded and also the one through which faeces are ejected as well as that through which food is taken in, so that the upper and smaller opening is comparatively functionless. The mantle is also tubular like the shell which it secretes; but in the young Scapho-

poda the mantle consists of right and left lobes like those of a Pelecypod and it is by the fusion of these that the tubular form is produced. We should therefore be justified in regarding the Scaphopoda as modified Pelecypoda, were it not for the fact that the Scaphopoda have a well-developed radula sac and complicated muscles for moving it, which constitute a buccal mass like that of the snail. There are likewise buccal ganglia connected with the cerebral ganglia by their own buccal commissure and the cerebral and pleural ganglia are quite distinct. These facts render it impossible to believe that the Scaphopoda are descended from the Pelecypoda and so they must be regarded as an independent division of the Molluscan phylum.

The Scaphopoda further possess neither labial palps nor ctenidia, and in this also they differ from every Pelecypod known. The mouth is surrounded by a star-shaped frilled membrane and at its sides are inserted two groups of mobile thread-like ciliated tentacles with thickened tips called captacula which Lankester regards as representing the missing ctenidia. How these act in capturing food is not known. The kidneys are two sac-like organs. The genital organ is a median mass of tubes occupying the posterior end of the animal, and it opens into the right kidney. There is no distinct heart but there is a pericardial space and a single longitudinal vessel in the roof of this may perhaps represent the heart. The genus *Dentalium* is fairly common round our coasts and may be dredged at moderate depths on a muddy bottom as in the Clyde area.

Class V. Cephalopoda.

The last class of the Mollusca, very differently constituted from the Lamellibranchiata, is that of the Cuttle-fish, or Cephalopoda. This paradoxical name, literally "head-footed" (Gr. κεφαλή, head; πούς, ποδός, a foot), is suggested by the circumstance that the foot has grown forward and upwards at each side of the head, and that these two extensions have met and coalesced, so to speak, on the back of the neck. The edges of this part of the foot, which may be called the fore-foot, are drawn out into strap-like processes, which are the arms by which the animal seizes its prey. The edges of the hinder part of the foot, on the other hand, have become bent round and joined beneath the animal, so as to form a tube, the funnel, through which water is ejected from the mantle-cavity.

The best known British Cephalopoda are the Squid, *Loligo forbesi*, often caught by trawlers, to whom it is known as the

Sepia.

"ink-fish"; *Sepia officinalis*, the Cuttle-fish, taken in

the English Channel and also abundant in the Mediterranean, where it is a favourite article of food; *Moschites cirrosa* with eight arms and a single row of suckers; *Polypus* (or *Octopus*) *vulgaris* almost confined to the south coast and commoner on the French shores and in the Mediterranean. Another Squid, *Ommatostrephes*, is common in the Gulf of St Lawrence and on the shores of the eastern United States.

The body of *Sepia* appears to be composed of a swollen head separated by a neck from a tapering trunk. When closely examined, however, the body is seen to be nothing but a long pointed visceral hump, like that of the snail, but it is not twisted and is not protected by an external shell. The mantle, as in the snail, is a skirt-like fringe of skin, the space between its inner surface and the visceral hump forming the large mantle-cavity. In order to compare the animal with the snail it must be placed with the point of the hump projecting upwards and backwards (Fig. 142). The so-called head includes the true head, with two enormous eyes of almost human aspect, surrounded by the fore-foot. The fore-foot is drawn out into eight short pointed arms, thickly covered on their inner sides with stalked suckers (Fig. 143), and two very long arms bearing suckers only at their expanded ends. These latter can be pulled back into two large pits situated at their bases, and when so retracted they are completely hidden from view.

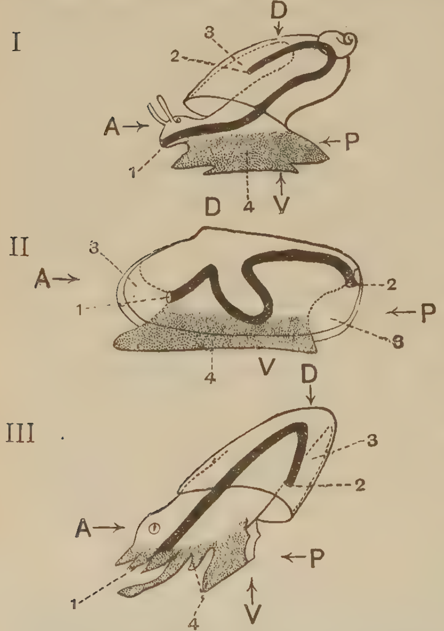

FIG. 142. Diagrams of a series of Molluscs to show the form of the foot and its regions and the relations of the visceral hump to the antero-posterior and dorso-ventral axes. After Lankester.

I. A Prosobranch Gastropod. II. Lamellibranch. III. A Cephalopod. A. Anterior surface. P. Posterior surface. D. Dorsal surface. V. Ventral surface. 1. Mouth. 2. Anus. 3. Mantle-cavity. 4. Foot.

The sucker is a cup with a horny rim which keeps the opening from collapsing. In its base there is a swelling, which is the end

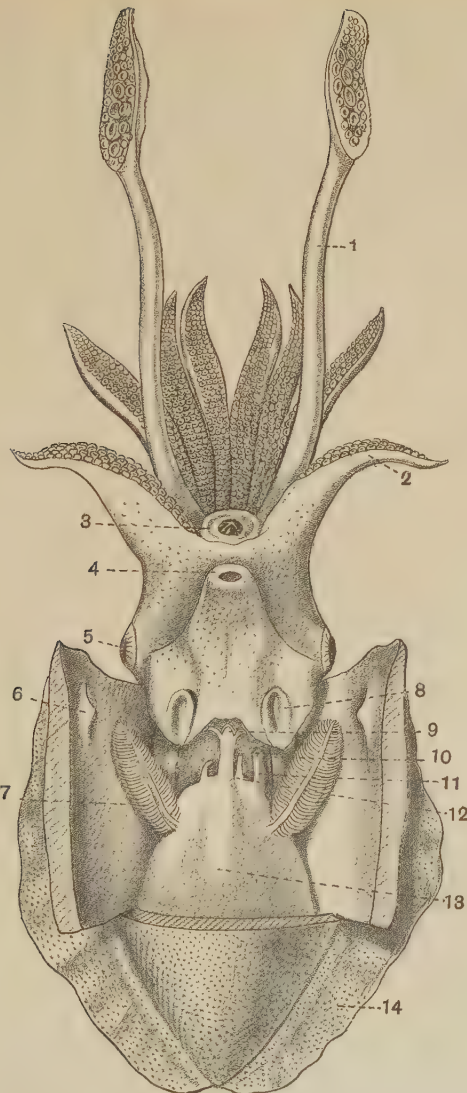

FIG. 143. Posterior view of male of *Sepia officinalis* × 1. The mantle-cavity has been opened to expose its contents.

1. Long arm half protruded. 2. A short arm; this one is hecto-cotylised. 3. Lips surrounding horny jaws; mouth. 4. External opening of funnel. 5. Eye. 6. Cartilaginous knob on mantle which fits into the socket 8. 7. Gill. 8. Socket for 6. 9. Anus. 10. Depressor muscle of the funnel. 11. Reproductive pore. 12. Right kidney papilla. 13. Visceral mass. 14. Fin.

of a muscle running into the stalk, and by the contraction of this, when the cup is applied to any object, a partial vacuum is produced. By means of the suckers the Squid can take a firm hold of its prey.

The hind-foot is the tube known as the funnel (Figs. 143 and 146). The posterior end of this is overlapped by the hind end of the mantle; in other words, it projects into the mantle-cavity. The mantle is very muscular; by the contraction of longitudinal muscles running towards the apex of the hump the mantle-cavity is widened; by the contraction of circular muscles it is narrowed, and by the alternate action of these two sets of muscles, water is sucked in and forced out of the mantle-cavity.

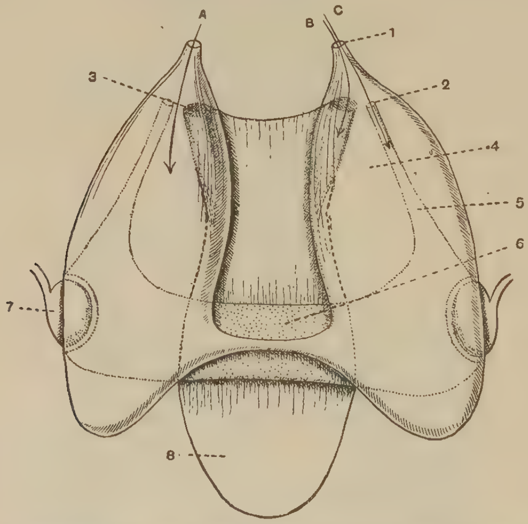

Fig. 144. A diagram showing the relation of the kidneys to the pericardium in *Sepia*.

1. External opening of the kidney into mantle-cavity. 2. Internal opening of the kidney into the pericardial coelom. 3. Opening of the right kidney into the dorsal sac and hence into the left kidney. 4. Left kidney, ventral portion. 5. Reno-pericardial canal. 6. Pericardium (part of the coelom). 7. Branchial heart. 8. Dorsal sac common to both kidneys. A. Arrow passing into left kidney by external opening from mantle-cavity. B. Arrow passing into right kidney through external opening into median lobe. C. Arrow passing into external opening and then into internal opening, and so into pericardial coelom. The extension of the coelom in which the generative cells arise is not shown in this diagram.

When, however, the mantle-cavity is contracted, two projecting pegs on the inner side of the mantle fit into sockets on the outer side of the funnel (6 and 8, Fig. 143). No water can then escape over the free edge of the mantle, and all is ejected in a narrow and forcible stream through the funnel. The funnel itself is muscular

and by contraction aids the process; there is a valve-like projection inside it which prevents water from being driven back into the mantle-cavity (Fig. 146).

Since water is sucked in gently and ejected forcibly the animal is propelled in the opposite direction, that is backwards, by the reaction of the stream against the surrounding water. *Sepia* can however also swim gently forward by wave-like undulations of the two lateral fins. These fins are flaps of skin projecting from the sides of the visceral hump (14, Fig. 143).

It has been said that the visceral hump is unprotected by an external shell. This is not strictly true. On the anterior surface of the hump there is an oval plate-like shell completely hidden in a sac formed by the meeting over it of upturned flaps of skin (14, Fig. 146). From its upper surface project an innumerable number of delicate calcareous plates parallel to one another, the spaces between them being filled with gas so as to give lightness.

In one or two living Cephalopoda, as for instance the Pearly Nautilus (*Nautilus pompilius*), and in very numerous extinct forms, there was a large tubular external shell which might be straight or coiled, but which always had the peculiarity of having a large number of septa or transverse plates dividing up its cavity into chambers, only the last of which contained the visceral hump, the rest being filled with gas (Fig. 149). In *Sepia* it is supposed that the chambers have become so small and shallow that the last one simply appears as a plate situated on part of the surface of the hump. The other chambers contain gas as in *Nautilus*.

Sepia possess two well-formed ctenidia, each consisting of an axis bearing two rows of thin plates. The axis is suspended from the body by a membrane, and the ctenidia project downwards instead of backwards as in the Lamellibranchiata (7, Fig. 143).

As in Lamellibranchiata, there are two kidneys, which open by little papillae placed just in front of the bases of the ctenidia (12, Fig. 143). Just inside the papilla is a narrow opening, the lips of which are folded so as to make it appear like a rosette. This is the internal opening of the kidney: it leads into a lateral prolongation of the pericardium, which is the reno-pericardial canal (5, Fig. 144). The kidney has the form of a wide sac and may perhaps be compared to a U-shaped kidney, like that of *Unio*, in which the two limbs have become merged in one another.

The wall of the kidney is smooth, except over the course of the large veins which run beneath its upper and inner wall. Here the

epithelium is folded and consists of tall cells which are actively engaged in extracting excreta from the blood, as is shown by the rows of granules with which they are filled. From the anterior ends of the kidney two outgrowths project which immediately fuse into one and constitute a great pouch called the dorsal sac (8, Fig. 144) stretching upwards and backwards just underneath the shell. This peculiar extension gives to the two kidneys the form of M, between the median V and outer limbs of which lies the pericardium. Posteriorly the cavities of the right and left kidneys also communicate with one another.

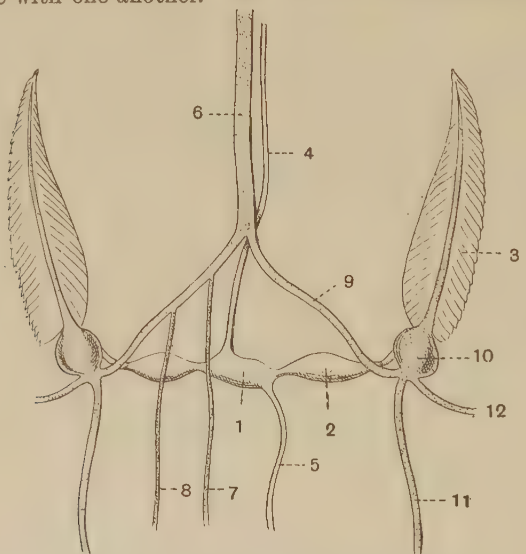

FIG. 145. View of heart and chief blood-vessels of *Sepia cultrata*. Partly after Parker and Haswell.

1. Ventricle. 2. Auricle. 3. Ctenidium. 4. Anterior aorta. 5. Posterior aorta. 6. Anterior vena cava. 7. Vein from ink-sac. 8. Genital vein. 9. Branchial vein. 10. Branchial heart. 11. Right abdominal vein. 12. Vein from the mantle.

The pericardium is a wide sac lying between the dorsal sac of the kidneys and their ventral parts. At the sides it gives off the reno-pericardial canals, whilst the stomach and intestine project into its roof.

The ventricle of the heart is a spindle-shaped sac lying transversely (1, Fig. 145). Into its two ends open the tubular thin-walled auricles which receive the blood from the ctenidia. From its anterior wall a powerful artery, the anterior aorta, is given off running forward above the oesophagus to the head, and a smaller artery or posterior aorta goes backwards and upwards to supply the

stomach and genital organ. These arteries have regularly formed branches from which the blood enters definite veins. This formation of well-defined channels for the blood is characteristic of the Cephalopoda. Of these veins the most important are: (1) the anterior vena cava; this is a channel in the mid-ventral line in front of the kidneys, which forks and sends a branchial vein over each kidney to the base of each gill; (2) the abdominal veins; these are a pair of large channels which come from the mantle, especially the upper part of it, and join the forks of the vena cava just before they enter the gills; (3) the genital vein; this is a trunk draining the genital organ, it runs along the posterior wall of the dorsal pouch of the kidney and joins the right fork of the vena cava; (4) a vein from the ink-sac joining the same fork, and (5) on each side a smaller vein from the mantle joining the main venous system at the branchial hearts (Fig. 145). Where these veins come in contact with the kidney wall the special excretory tissue mentioned above is developed.

A peculiar feature in the circulatory system is the presence of a pair of muscular swellings of the forks of the vena cava just before they enter the gills. These are the branchial hearts, the function of which is to drive the blood into the gills, whereas the auricles drain it out of them. Each branchial heart projects on the one side into the kidney and on the other side into the reno-pericardial canal, and the epithelium of the latter where it covers the heart is greatly thickened so as to form a cushion, the function of which is excretory. This, like Keber's organ in the river-mussel, is a remnant of the primitive excretory function which probably all the cells of the coelom once possessed.

The alimentary canal of *Sepia* is constructed on very much the same plan as that of the snail. The mouth is situated in the centre of the arms and surrounded with a frilled lip (Fig. 143). There is a large buccal mass containing the radula and there are a pair of powerful jaws shaped like a parrot's beak, movable on one another of which the ventral is the larger. There are two salivary glands and a long narrow oesophagus but no crop. The oesophagus widens behind into the stomach, which receives, as is usual in Mollusca, the ducts of the liver. With the stomach is connected a side pouch spirally coiled. The liver is enormous, occupying all the anterior portion of the visceral hump; the ducts traverse the dorsal extension of the kidneys, and are in this position covered externally with excretory tissue, which by the older naturalists was termed "pancreatic" caeca (12, Fig. 146) from a mistaken comparison with the human pancreas. The intestine is slightly bent on itself and

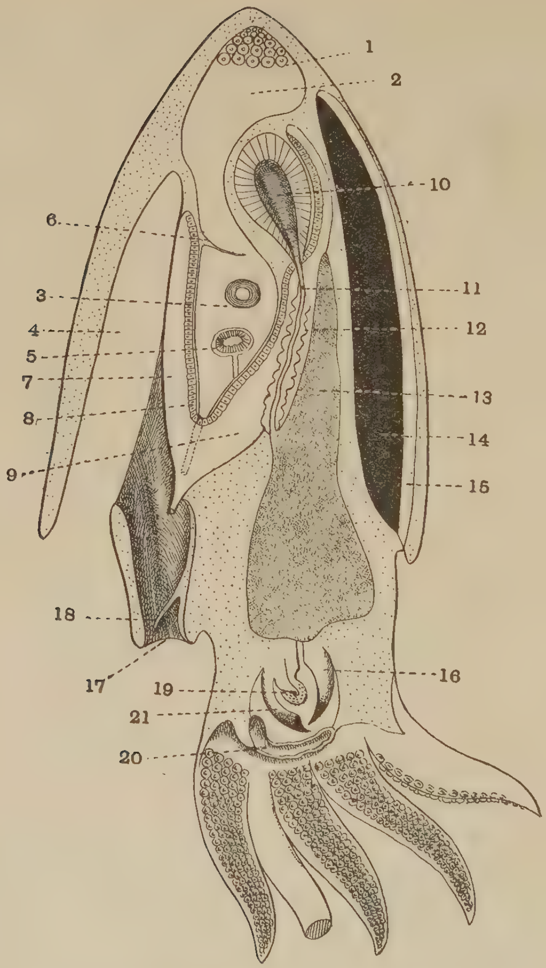

FIG. 146. Left half of a *Sepia*, showing the relation to one another of some of the principal viscera, × about 1. Diagrammatic.

1. Ovary. 2. Genital part of the coelom. 3. Pericardial part of the coelom; the reference line touches the heart. 4. Mantle-cavity. 5. Section of intestine. 6. Incomplete septum between genital and pericardial coelom. 7. Ventral limb of kidney. 8. Glandular tissue of kidney. 9. Dorsal limb of kidney. 10. Stomach. 11. Liver duct. 12. "Pancreatic" caeca. 13. Liver. 14. Shell. 15. Shell sac. 16. Dorsal horny jaw. 17. Anterior opening of funnel. 18. Valve in funnel. 19. Radula. 20. Lips. 21. Ventral horny jaw.

ends in an oval papilla. A peculiar sac, the ink-sac, the cells lining which secrete the pigment known as Indian ink or Sepia, opens by a long duct on this papilla (Fig. 148). When the Cuttle-fish is alarmed it ejects this ink and darkens the water so much as completely to escape from view.

The nervous system consists of ganglia even more closely massed than in the case of the snail. The supra-oesophageal ganglia form one rounded mass; they are produced at the sides into the very much larger optic ganglia which are in close relation to the eyes (Fig. 147). The pedal ganglion is divided into an anterior ganglion called the brachial, and a posterior ganglion sometimes called the infundibular. The brachial ganglion supplies a stout nerve to each arm, and each nerve swells out into a small ganglion

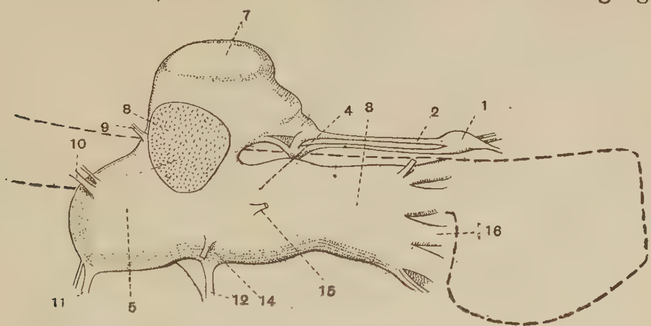

FIG. 147. Lateral view of the central nervous system of *Sepia officinalis*. Magnified. From Cheron.

1. Upper buccal ganglion. 2. Nerves connecting buccal ganglion with cerebral ganglion. 3. Brachial ganglion. 4. Infundibular ganglion. 5. Pleural ganglion. 7. Supra-oesophageal ganglion. 8. Cut end of optic nerve. 9. Superior ophthalmic nerve. 10. Pallial nerves. 11. Visceral nerve. 12. Anterior nerve to the funnel. 14. Auditory nerve. 15. Inferior ophthalmic nerve. 16. Nerves to the arm. The dotted outline represents the buccal mass and the oesophagus.

just where it enters the arm (Fig. 148). The infundibular ganglion supplies the funnel.

Posterior to the infundibular ganglion are the two pleural ganglia fused together. These give rise to a visceral loop which supplies the various internal organs and the gills. From the same ganglion two short nerves run to the mantle and terminate in the two large stellate ganglia, which underlie the skin and supply nerves to all the muscles of the mantle (Fig. 148). In all Gastropoda pallial nerves which supply the mantle arise from the pleural ganglia, but in *Sepia*, owing to the mobility and muscularity of the mantle, the great stellate ganglia are developed in connection with these nerves. The buccal mass is supplied by two ganglia,

superior and inferior, each representing a pair fused together, they are joined by a minor nerve collar running round the oesophagus. The inferior ganglion corresponds to the buccal pair in the snail, the superior is a separated part of the cerebral.

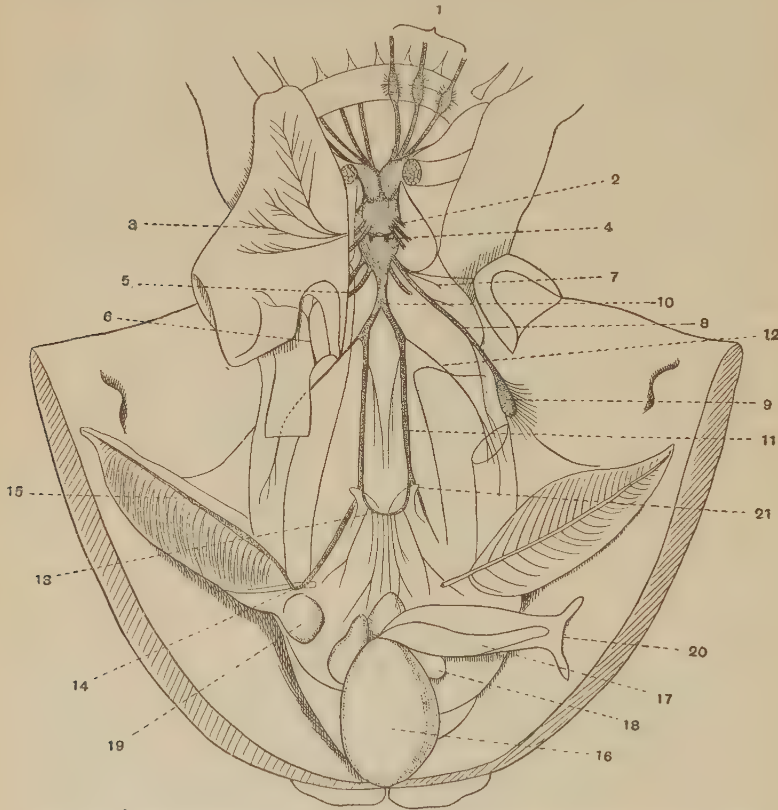

FIG. 148. *Sepia officinalis* dissected to show the nervous system, ventral view. From Cheron.

1. Three nerves to the arms dissected out. 2. Auditory nerve. 3. Anterior nerve to the funnel. 4. Nerve to vena cava. 5. Posterior nerve to funnel. 6. Continuation of this nerve. 7. Accessory nerve to mantle. 8. Left nerve to mantle. 9. Stellate ganglion. 10. Common trunk of the visceral loop. 11. Left branch of the visceral loop. 12. Nerve to muscles. 13. Nerve to viscera. 14. Ganglion on branchial heart. 15. Nerve of ctenidium. 16. Ink-sac. 17. Duct of ink-sac. 18. Left nidamental gland. 19. Branchial heart. 20. Position of anus. 21. External opening of kidneys.

It has been already stated that *Sepia* possesses complicated eyes. In the embryo these, like the eyes of the snail, are merely sacs lined by visual cells and containing a transparent horny secretion which serves as a lens. In fact, in the embryo, the sac is at first a pit

which gradually closes up. Immediately over the spot where the first pit closed a second pit is formed in which a second horny lens is formed just over the first one, so that the lens consists of two pieces, and as in the eye of the Vertebrate, there is an anterior and a posterior chamber in the eye separated from one another by the lens.

Into the anterior chamber a circular fold projects called the iris, fulfilling exactly the same function as the iris of the human eye or the diaphragm in a photographic camera. Outside and around the eye a circular fold acts as an eyelid.

The cerebral, pedal and pleural ganglia are surrounded by very tough connective tissue, in which the fibres, although still visible, are cemented together by a material of cheesy consistence, and this type of tissue is called fibro-cartilage. In this way a kind of skull is formed, which sends a scoop-like extension on either side over the back of the eye, covering the optic ganglia. The edges of the scoop pass into ordinary connective tissue round the rest of the eye. This tissue forms the wall of the eyeball.

The otocysts are branched and embedded in the ventral wall of the skull. They receive nerves from the cerebral ganglia, but as these nerves traverse the pedal ganglia they appear to arise from the latter.

The genital organ in *Sepia* occupies the apex of the visceral hump. It is, as examination of young specimens shows, a thickening of the wall of the coelom, behind the pericardium. The coelomic space into which the eggs and spermatozoa are shed is only shut off from the pericardium by an incomplete partition, so that in *Sepia* a state of things persists throughout life which is found only in the embryos of some other forms (Fig. 146).

The genital duct is present only on one side, the left, and is produced into a prominent papilla which in the male is used as a penis (Fig. 143). The outermost part of the duct in the male is a wide pouch in which the spermatozoa are welded into masses and enveloped in cylindrical cases called spermatophores. Just inside this the duct receives the excretion of two glands termed prostate glands; further inwards it narrows into a very fine tube which opens internally into the coelom. Since in some cuttle-fish the genital duct is paired and in *Nautilus* there are two pairs of kidneys, while the genital ducts of that animal appear to be portions of the anterior kidney ducts split off, it has been suggested that the genital duct of *Sepia* is all that is left of a missing pair of kidneys. Close examination of a male *Sepia* will show that the base of one of the short arms is modified because it is somewhat broader than the rest and the suckers have a tendency to be obliterated. In

fertilizing the female the male inserts this arm into his own mantle-cavity and receives on to it the spermatophores from his own genital duct. He then inserts it in the mantle-cavity of the female and deposits the spermatophores in a depression of her skin either on the head or near the opening of the oviduct. In other genera such as *Argonauts* the modification of this arm is much more pronounced —the basal portion loses its suckers and is converted into a sac. During copulation this arm is amputated and left in the mantle-cavity of the female. It was found there by Cuvier who mistook it for a Trematode worm and called it Hectocotylus (literally hundred suckers). Hence this arm in all genera even in *Sepia* where the modification is slight is termed the hectocotylized arm.

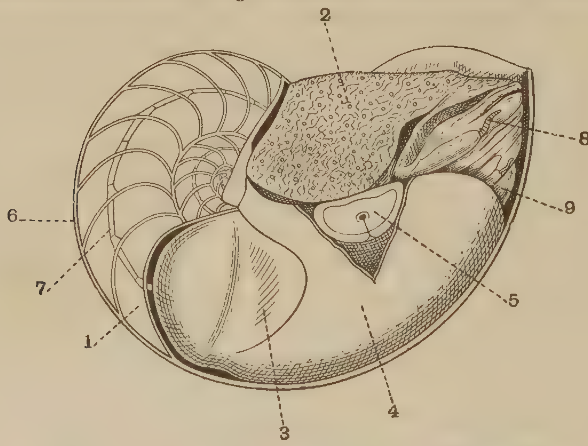

FIG. 149. Side view of *Nautilus pompilius* × ½. After Graham Kerr. Half the shell has been removed to expose the animal and the chambers of the shell.
1. Last completed chamber of the shell. 2. Hood part of foot. 3. Shell muscle. 4. Mantle cut away to expose (5) the pin-hole eye. 6. Outer wall of shell, some of which is cut away to show the chambers. 7. Siphon. 8. Tentaculiferous lobes of the foot. 9. Funnel.

The oviduct is simple, but in the female there are four glands, the nidamental glands, situated on the wall of the mantle cavity just outside the kidneys (18, Fig. 148). From the secretion of these glands tough egg-shells resembling india-rubber cases are made. The egg is about the size of a pea and when the young cuttle-fish emerges it is already like the adult.

Cuttle-fish feed chiefly on crabs, shrimps and other Arthropoda, using their beaks to break the hard shell. Some are large enough to attack men and this circumstance has given rise to many legends. Gigantic species are sometimes cast dead on the shores of Nova Scotia, the length of body being ten feet, and of the arms over fifty feet. The phylum Mollusca finds its climax in the cuttle-fishes.

Modern cuttle-fish have a fairly uniform structure. The two long tentacular arms are absent in the Octopoda. In *Loligo* the shell is horny, in *Polypus* it is entirely absent. In *Ommatostrephes*, the common cuttle-fish of the Gulf of St Lawrence, the anterior chamber of the eye is open and the lens bathed with sea-water.

Nautilus.

Nautilus is a remarkably interesting cuttle-fish, widely different from *Sepia* and the others, but closely allied to most of the extinct forms. The arms are short, broad, ill-defined lobes, the suckers being represented by tentacles with raised ridges round their bases. There is a large external shell coiled forwards in the median plane over the animal's head, so to speak (Fig. 149). The visceral hump is enclosed in the last chamber and from the apex of the hump a membranous tube called the siphuncle is given off, which runs through all the other chambers, piercing the septa. There is a fold of the mantle turned back over the anterior edge of the shell, the first foreshadowing of the shell-sac of *Sepia*.

There are four gills and four kidneys and four auricles in the heart. Thus *Nautilus* shows traces of segmentation. The papillae of the posterior kidneys are split, one half leading directly to the reno-pericardial canal, the other into the sac-like kidney. The reno-pericardial canals thus open directly to the exterior, and the genital ducts are in such a relation to the anterior kidneys as to make it probable that they are the reno-pericardial canals belonging to these, which have acquired independent communication with the exterior.

Phylum MOLLUSCA.

Mollusca are classified as follows:

Class I. Gastropoda.

Mollusca with a flat foot adopted for crawling. There is a buccal mass and radula; distinct pleural ganglia are present and the shell is never composed of paired pieces.

Sub-class I. Isopleura.

Bilaterally symmetrical Gastropoda with a shell composed of eight median plates situated in a longitudinal series. Numerous pairs of ctenidia.

Ex. *Chiton.*

Sub-class II. Anisopleura.

Asymmetrical Gastropoda, with the left side of the visceral hump long in comparison to the right, the anus, kidneys and ctenidia being shifted forwards.

Division I. Streptoneura.

The anus and ctenidia shifted so far forward that the visceral loop is pulled into the shape of an eight and the gill is anterior to the heart.

Order 1. **Aspidobranchiata.**

Usually two kidneys, two auricles, two ctenidia. The axis of the ctenidium free and both rows of plates present.

Ex. *Haliotis*, *Patella*.

Order 2. **Pectinibranchiata.**

One kidney, one auricle, one ctenidium of which the axis is adherent to the mantle and only provided with one row of plates.

Ex. *Buccinum*, the Whelk.

Division II. EUTHYNEURA.

The visceral loop is untwisted and the gill is posterior to the heart.

Order 1. **Opisthobranchiata.**

Marine Euthyneura with open mantle cavity in which a ctenidium is often present.

Ex. *Aplysia*.

Order 2. **Pulmonata.**

Land and fresh-water Euthyneura breathing air, having the mantle cavity converted into a lung and the ctenidium aborted.

Ex. *Helix*.

Class II. LAMELLIBRANCHIATA (PELECYPODA).

Mollusca with a shell composed of two valves united by a hinge, and a mantle of two lobes. The foot is usually wedge-shaped and the plates of the ctenidia are fused to form gill-plates. No buccal mass. Pleural ganglia fused with the cerebral.

Sub-class I. PROTOBRANCHIATA.

Small Lamellibranchiata with a simple ctenidium like that of Gastropoda, and large labial palps.

Ex. *Nucula*.

Sub-class II. FILIBRANCHIATA.

Lamellibranchiata in which the filaments of the ctenidium are loosely united with one another and their bent-up ends are not united to the mantle.

Ex. *Mytilus*.

Sub-class III. Eulamellibranchiata.

Lamellibranchiata in which the filaments of the ctenidium are welded into a "lamella" or plate and their bent-up ends are joined to the mantle.

Ex. *Unio, Anodonta.*

Class III. Solenogastres.

Degenerate worm-like Mollusca devoid of shell and foot and with a ventral ciliated groove. There is a rudimentary radula and the genital organs burst into the pericardium, the kidneys serving as genital ducts.

Ex. *Chaetoderma, Neomenia.*

Class IV. Scaphopoda.

Mollusca with a tubular shell and mantle and a long cylindrical foot ending in three processes. A buccal mass and pleural ganglia are present. The genital organ opens into the right kidney.

Ex. *Dentalium.*

Class V. Cephalopoda.

Mollusca in which the front part of the foot surrounds the head and is drawn out into sucker-bearing arms whilst the hind portion of the foot forms a muscular tube. The ganglia are massed together and protected by a skull: there is a buccal mass with a radula and two jaws.

Sub-class I. Tetrabranchiata.

Cephalopoda with four ctenidia, four kidneys, four auricles, a large external shell, no suckers and very short arms.

Ex. *Nautilus.*

Sub-class II. Dibranchiata.

Cephalopoda with two ctenidia, two kidneys and two auricles. The shell is enveloped in the mantle and the arms are long and provided with suckers.

Order I. **Decapoda.**

Dibranchiata with two long and eight short arms.

Ex. *Ommatostrephes, Sepia.*

Order II. **Octopoda.**

Dibranchiata with eight arms of equal length.

Ex. *Polypus* (*Octopus*).

GLOUCESTER

CHAPTER XIV

PHYLUM ECHINODERMATA

The class of animals known as the Echinodermata comprises the well-known Star-fish or Five-fingers, the equally well-known Sea-urchins, the less familiar Sea-cucumbers and Brittle-stars, lastly the graceful Feather-stars. The name is derived from two Greek words, ἐχῖνος, which means hedgehog (and was also used for the sea-urchin), and δέρμα, the skin. The prickles and spines with which many members of this Phylum are covered constitute a very prominent feature in their appearance. Spines, it is true, are sometimes absent, but in every case, whether this is so or not, the skin contains a skeleton consisting either of plates or of rods, and the spines are merely rods belonging to this skeleton which project outwards and are still covered by the skin which they push before them.

Class I. Asteroidea.

The most familiar of all the British Echinoderms is probably the common star-fish, *Asterias rubens*, which may be found at low water on almost any part of the coast where shell-fish, its favourite food, abound. Very similar species, *Asterias vulgaris* and *Asterias polaris*, abound on the American coast, the first-named on the New England coast, the second further north in the Gulf of St Lawrence. The species represented in Fig. 150 belongs to a different genus, *Echinaster*, but in all essential features of its anatomy it agrees with *Asterias*. *Echinaster sentus* is common on the N. American coast. The name "star-fish" denotes that the shape resembles the conventional figure of a star. The body is produced into five arms or lobes which are arranged like the spokes of a wheel round the centre of the body or disc, on the under side of which the mouth is situated. These arms are termed radii, and the re-entrant angles between them interradii.

The star-fish creeps about with its mouth downwards: its motion is effected by means of numerous delicate semi-transparent tentacles. These are situated in five grooves which run along the under side of the arms and converge towards the mouth, where they merge into a depression

Skeleton.

FIG. 150. Oral view of *Echinaster sentus* with tube-feet extended × about 1. From Agassiz.

surrounding that opening. These grooves are termed the ambulacral grooves: the tentacles situated in them are called the tube-feet, and the depressed space round the mouth in which all the grooves unite is called the buccal membrane (Lat. *bucca*, the cheek) or the peristome (Gr. περί, around, and στόμα, mouth).

So far as we have yet seen the Echinoderms seem to differ from Coelenterates, which are also radiate animals, in the details of the arrangement of the organs rather than in any fundamental features. The skeleton no doubt is peculiar in being embedded in the skin: but the spicules of the Alcyonaria occupy a similar position, although they rarely cohere to form the definite rods and plates like those characteristic of Echinoderms. When the soft parts are dissolved away from one of these rods or plates by caustic potash it is seen to consist of a delicate network of calcium carbonate; and it is found by observation of the developing young that such a plate is formed by a little heap of cells coming together and secreting a calcareous rod between them: this rod then branches at both ends and the branches bifurcate again so that the twigs of the second or third degree approach each other and joining form a mesh, and this process of bifurcating and joining is repeated until the plate or spine is built up. The growth of the primitive rod into the meshwork is rendered possible only by the growth of the cells which shed out the calcium carbonate. These cells remain throughout life, more or less modified, as a kind of living network interpenetrated by the skeletal one.

Coelom.

When however we cut a star-fish open we see that the animal apparently consists of two sacs placed one within the other. The innermost sac or alimentary canal opens in the centre of the upper surface by a minute opening, the anus, through which undigested matter is thrown out, and on the under surface by the mouth. The space or sac which apparently surrounds the digestive cavity of the star-fish is a true coelom: like the coelom in a segment of an Annelid it has been formed by the union of two sacs which in the embryo lay right and left of the digestive tube. From its walls the muscles are developed, the generative cells, and also the cells which give rise to the skeleton. Between the outer wall of the body-cavity and the true external skin which corresponds to the ectoderm, there is a mass of more or less gelatinous substance exactly corresponding to the jelly of a Medusa or the connective tissue of an Arthropod, which constitutes the substance of the body-wall. Into this material wander cells budded from the wall of the coelom: these cells from their power of movement and appearance can be recognised as amoebocytes. It is from these cells that the skeleton is formed in the way we have described above: some of them, however, retain their primitive character and wander about, probably carrying food to the various

parts of the body-wall or perhaps carrying away waste matter. A third section again secrete the fibres which bind the various rods constituting the skeleton together and thus form a simple and primitive variety of connective tissue.

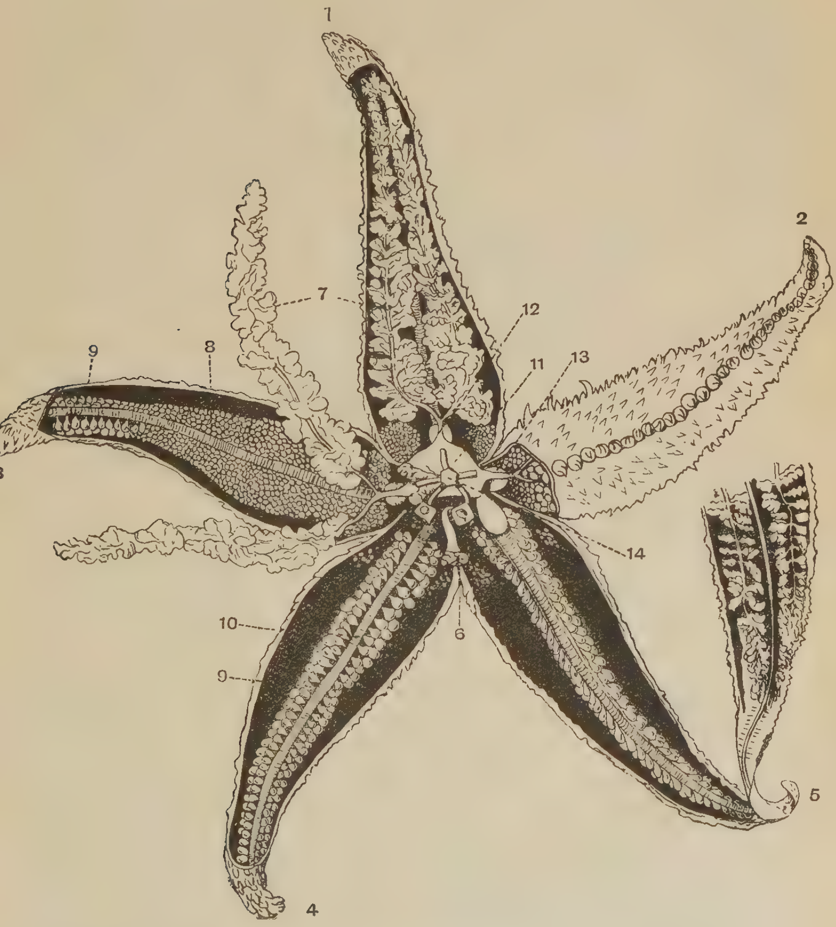

Fig. 151. The common Star-fish, *Asterias rubens*, dissected to show motor, digestive and reproductive systems. After Rolleston and Jackson.

1—5. The five arms. 6. Madreporic plate and canal. 7. Arborescent "hepatic" caeca, two in each arm. 8. Generative organs. 9 Ampullae of tube-feet. 10. Ambulacral plates, inner surface. 11. Pyloric sac. 12. Duct leading from pyloric sac to pyloric caeca. 13. Stomach bulging into arm. 14. Anus.

Alimentary canal.

The alimentary canal can most easily be examined by carefully removing all the upper parts of the five arms in one piece; this is done by cutting along both sides of each arm, then raising the upper part of the animal and clipping through the intestine near the anus. By this means the animal is separated into an upper and lower half and all the internal organs are displayed in one piece or the other. The alimentary canal is then seen to consist of several regions clearly distinguished from one another. It begins with an exceedingly short gullet which passes at the lips into the buccal membrane already mentioned: the gullet widens out above into a very loose baggy stomach which is produced into ten short pouches, two situated at the beginning of each arm. Above the stomach and communicating with it by a wide aperture lies a flattened pentagonal bag, called the pyloric sac, and from each of the five angles of this sac there is a tube given off which runs into each arm, where it is soon divided into two parallel sacs, each produced into a multitude of little, short pouches. These sacs are called the pyloric caeca: caecum, Latin "blind," being a convenient zoological term for a blind pouch. Each of the pyloric caeca is tied to the upper side of the arm, by two bands of transparent membrane called mesenteries. From the centre of the pyloric sac a short straight tube runs to the upper surface of the animal where it opens by a minute anus: this tube is called the rectum, a name, as we have seen, commonly given to the last portion of the digestive tube. The rectum has attached to it two branched tubes of a brown colour which open into it, called the rectal glands.

The reason of the division of the digestive sac into various parts is of course the different uses to which they are put in the life of the animal; and we may stop for a moment to enquire what these uses are.

Star-fish feed chiefly on bivalve shell-fish, such as mussels, cockles and clams, though they will attack almost any animal which they can catch. Their mode of seizing their prey is very curious. If they are attacking a bivalve, they bend all their five arms down round it, thus arching up the central portion of the body (Fig. 152). Then the stomach is pushed out,—this being rendered possible by the turning inside out of its edges, which, as we saw above, are loose and baggy—and wrapped around the fated mollusc. The pushing out is effected by the contraction of some muscle fibres in the body-wall: these tend to diminish the space

which the coelom occupies, and as this is filled with incompressible fluid, the stomach must be pressed out. After some time has elapsed the star-fish relaxes its hold and it is then seen that the shell of the mollusc is completely empty and as clean as if it had been scraped with a knife. It was long a puzzle how the star-fish succeeded in forcing its victim to relax its muscles and allow the valves to open. It was supposed that the stomach secreted a paralysing poison, but it has been conclusively proved that this is not the case, but that the star-fish drags the valves of its victim apart by main force, often actually breaking the adductor muscles. By assuming the bunched up position shown in Figure 152 the

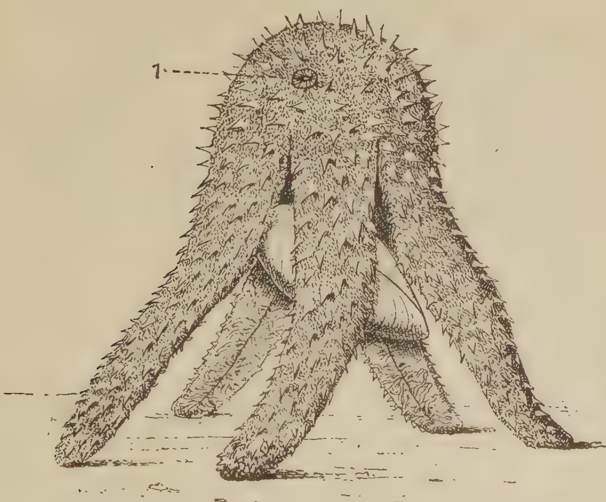

Fig. 152. *Echinaster sentus*, in the act of devouring a mussel.
1. Madreporic plate.

star-fish is enabled to use the tube-feet of opposite arms to pull on the valves of the victim in opposite directions. The pull exercised by the suckers is not nearly strong enough to open the valves at once, but the star-fish has staying power and eventually the mussel is slowly forced open. The cells lining the stomach include a large number of goblet-cells (v. p. 151) swollen by drops of clear fluid; those of the pyloric sac, on the other hand, present a different appearance. These are full of minute granules and recall the appearance of the cells in other animals which contain the active digestive principle. Hence it seems reasonable to suppose that the mussel is digested by the secretion of the pyloric sac and its

appendages, which flows downwards into the stomach. Any portion remaining undigested is expelled through the rectum; no food ever penetrates into the pyloric caeca.

The locomotion of the star-fish is effected in the following manner. The tube-feet which crowd the ambulacral grooves are during life continually extended and retracted. At their ends are flat circular discs, and these discs are pushed against the stone or rock or whatever else the star-fish is

Water-vascular system.

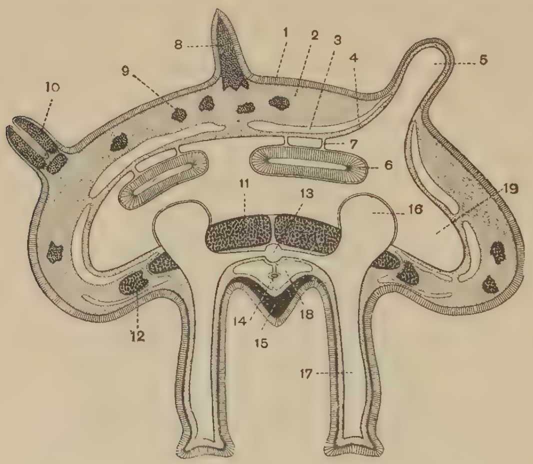

Fig. 153. Diagram of a transverse section of the arm of a Star-fish.

1. Ectoderm. 2. Jelly. 3. Peribranchial space in the skin. 4. Peritoneal lining of body cavity. 5. A branchia. 6. Pyloric caecum. 7. Mesentery supporting a caecum. 8. Spine. 9. Ossicle in skin. 10. Pedicellaria. 11. Ambulacral ossicle. 12. Adambulacral ossicle. 13. Radial trunk of water-vascular system. 14. Radial septum separating the two perihaemal spaces. 15. Radial nerve-cord, a thickened band of ectoderm with a plexus of nerve-fibrils underlying it. 16. Ampulla of tube-foot. 17. Tube-foot. 18. Perihaemal space. 19. Coelom.

clinging to. Then by the contraction of their muscles the centre of the disc is pulled upwards, and so it is made to adhere in exactly the same way in which a boy makes a leather "sucker" adhere to a stone. When once the disc is firmly fixed the contraction of the tube-foot draws the animal after it. This description applies to the movements of the star-fish when it is climbing, but when it is walking over level ground the tube-feet are used just like the legs of a man in walking, i.e. they push against the ground, they are then withdrawn, swing forward, and push again. The direction in which the star-fish moves is determined by the direction of the

swing which is parallel to the same line in all the arms, not necessarily parallel to the axis of the arm to which the tube-feet belong.

We found that in order to examine the alimentary canal it was advisable to divide the star-fish into an upper and a lower half. If we now cut away the tube-feet and look at the roof of the ambulacral groove from which they project, it will be seen that the groove is roofed in by a double series of calcareous rods, meeting each other at an angle like the beams of a church-roof (11, Fig. 153). These are called the ambulacral ossicles. They can be drawn together by muscle fibres running from one of a pair to its fellow just under the spot where they meet. By this action the ambulacral groove is narrowed; and at the same time, inwardly projecting spines lining its edges are made to meet, so that the tube-feet are entirely protected by a trelliswork of spines. The spines are attached to rods, called the adambulacral ossicles, which are firmly bound to the outer edges of the ambulacral ossicles (12, Fig. 153). Inside the animal, between the ambulacral plates, a series of pear-shaped transparent bladders tensely filled with fluid project into the coelom (Figs. 151 and 153). These are really the swollen upper ends of the tube-feet and are termed ampullae. They act as reservoirs into which the fluid contents of the lower part of the foot are driven when the longitudinal muscles of the tube-foot contract. The bladder-like upper end of the foot has only circular muscles, and when these contract the fluid is driven back into the lower part of the tube-foot and this is thus expanded. The tube-feet are really all parts of one system, though from the above description it would seem as if each was capable of acting without the others: but they are connected by short transverse tubes, with a canal running along the whole length of the arm immediately under the ambulacral ossicles, called the radial water-vessel (13, Fig. 153). This canal and its branches can easily be seen in microscopic sections of the arms of young star-fish, or they can readily be demonstrated by cutting off the tip of the arm of a fully-grown specimen, finding the end of the radial tube on the cut surface and injecting it with coloured fluid by means of a fine pipette. The five radial tubes are connected with each other by a ring-shaped canal lying just within the peristome, which is called the water-vascular ring. There are nine small pouches called Tiedemann's bodies projecting inwards from the ring canal. In these are formed the amoebocytes which are found floating in the fluid of the canal, and which arise by budding from the wall of each pouch.

From the ring canal also in one interradius, where the tenth Tiedemann's body if it existed would be found, a tube is given off which leads to the upper surface of the disc, where it opens by a sieve-like plate, pierced by numerous minute pores, called the madreporite (Figs. 151 and 152). This vertical tube receives the awkward name of the stone-canal because its walls are stiffened by calcareous deposit; its cavity is reduced to a mere slit by the projection into it of an outgrowth of its wall shaped in section like a Y with coiled ends, which is also strengthened by lime. Although, as we have said, the cavity of the stone-canal is a mere slit, yet it is lined by long narrow cells carrying most powerful cilia. In many species of star-fish, although not in *Asterias*, stalked sacs resembling greatly enlarged ampullae are attached to the water-vascular ring. These appear to act as reservoirs of fluid for it: they are known as Polian vesicles after Poli, the naturalist who first described them.

Now since all the movements of a tube-foot can be accounted for by the action of the longitudinal muscles of its lower part and the circular muscles of the ampulla, the question arises as to what is the purpose of this apparatus of radial and circular tubes, stone-canal and madreporite. There is one interesting little mechanism which supplies a valuable clue to the answer to this question. This is a pair of valves placed in the tube-foot at the entrance of the transverse canal, which unites it with the radial tube. These valves swing open into the tube-foot when the pressure in the radial tube is greater than the pressure in the tube-foot, but when the pressure in the latter is higher they close, so that under no circumstances can water escape from the tube-foot into the radial canal. So it appears that there is an arrangement which allows fluid to pass into the tube-foot but which prevents its return, and this implies that under ordinary circumstances there must be a loss of fluid from the tube-foot. We must in fact suppose that when the tube-foot is driven out by the contraction of the ampulla, the contained fluid slowly transudes through its thin walls and the loss is supplied from the radial canal. The pressure in the radial and circular canals is kept up by the action of the cilia in the stone-canal, by means of which a slow but steady current is produced, setting in from the outside through the madreporite.

The function of the whole system of tubes therefore is to keep the tube-feet full of fluid and thus tense and rigid, so that they can perform their functions properly.

The nervous system of the star-fish is one ot the most interesting features in its anatomy. The ectoderm consists of long delicate cells bearing flagella and interspersed with goblet-cells similar in appearance to those lining the stomach. The slime which these cells manufacture covers the surface of the animal and no doubt protects it from the attacks of bacteria and microscopic algae. But the chief point of interest is that at the bases of the long delicate cells there is an indescribably fine tangle of delicate nerve-fibres which are doubtless outgrowths of some of the cells. Here and there a nucleus is seen amongst them which belongs to a neuron—that is, an ectoderm cell which has lost its connection with the rest and has become pushed down into the fibrillar layer. The ectoderm all over the body is therefore underlain by a nervous sheath and is very sensitive, but there are certain places where the nervous sheath becomes very much thickened and it is these areas which constitute the true sense-organs and the central nervous system.

Nervous system.

Isolated sense-cells, that is, cells having a stiff protruding hair, are scattered all over the surface; but the only spot where they are collected in groups so as to form the sense-organs is on the tips of the tube-feet. The tube-feet are then practically the only sense-organs, and since the radial water-tube ends at the tip of an arm in an unpaired tube-foot devoid of a sucker, we might regard the whole radial tube as a huge, branched, sensitive tentacle. There is the more justification for doing this when it is found that the radial tube with its freely projecting tip is in the young star-fish quite independent of the outgrowth of the body called the arm, and only secondarily becomes applied to it. At the base of the end-tentacle there is a thick cushion of nervous matter in which are excavated a number of ectodermal pits lined by cells containing orange pigment. These pits are organs of vision: and it has been experimentally shown that a star-fish deprived of these organs is insensible to light.

The central nervous system consists of five thick bands of nervous tissue situated one above each ambulacral groove underneath the radial water-tube (Fig. 153). They are termed the radial nerve-cords and are joined together by a circular band of a similar nature, called the nerve-ring, lying under the water-vascular ring. Intervening between the radial nerve-cord and the radial water-tube there are two canals lined by flattened cells and separated from one another by an imperfect septum (14, Fig. 153). They are called

the radial perihaemal canals and are outgrowths from the coelom. From their upper walls are derived the muscles which move the ambulacral ossicles on one another: from their lower walls a layer of ganglion cells and nerve-fibres is developed, which may be termed the coelomic nervous system in order to distinguish it from the main mass of ganglion cells and fibres which are derived from the ectoderm. This coelomic nervous system, which is very thin in the star-fish, seems to serve as the channel by which impulses from the radial nerve-cord reach the ambulacral muscles. The five pairs of radial perihaemal canals are connected with one

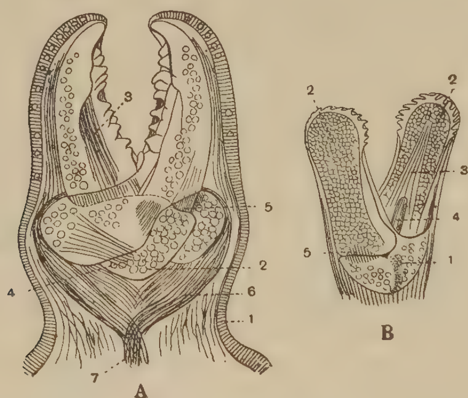

Fig. 154. Pedicellariae from *Asterias glacialis*. From Cuénot.

A. Crossed form × 100. 1. Ectoderm. 2. Base of left "jaw." 3. Muscle closing the "jaws." 4. Basal ossicle. 5. Muscle opening the "jaws." 6. Fibrous band connecting the basal ossicle with one of the rods of the skeleton. 7. Fibres of peduncle.

B. Straight form. 1. Basal ossicle. 2. "Jaws." 3. Adductor muscle. 4. Muscle closing the "jaws." 5. Muscle opening the "jaws."

another by a circular canal lying above the nerve-ring called the outer perihaemal ring. Inside this is another circular canal called the inner perihaemal ring, which is an expansion of the foot of the axial sinus (see p. 338).

Pedicellariae.

The upper or aboral surface of the star-fish is provided with two most interesting groups of organs, pedicellariae and dermal branchiae. The former are minute pincers, composed of two or rarely three blades moving on a basal piece. These close when the skin of the back is irritated; their main purpose appears to be to keep the surface of the animal clear from

germs of sessile animals and plants. They cover the thickened bases of the blunt spines with which the back is beset. Larger pedicellariae are scattered in the interspaces between the spines and are distinguished from the smaller by the fact that the blades do not cross as is the case with these. The larger kind are also found on the adambulacral spines.

The pedicellariae are probably little spines of the second order. In the small blunt-armed star-fish, *Asterina gibbosa*, there are no true pedicellariae, but the plates on the back bear small spines arranged in twos or threes, which act somewhat like pedicellariae when the skin is irritated.

Branchiae.

The dermal branchiae (5, Fig. 153) are conspicuous in a star-fish when alive; they are very difficult, on the other hand, to detect in preserved specimens. They are in fact thin spots on the body-wall, where it consists only of the ectoderm and the wall of the coelom closely apposed, the jelly, fibres and skeletal rods being absent. These spots project like little finger-shaped processes and their purpose is to facilitate respiration. The fluid in the coelom or body-cavity being here separated from the external water by a very thin membrane, the dissolved oxygen is able to pass from the one fluid to the other with great ease.

There is no localised excretory organ in the star-fish or indeed in any Echinoderm. Throughout the phylum so far as is known this function is performed by the amoebocytes which float in the coelomic fluid and have been produced by the budding of the cells forming the wall of the coelom. When charged with excreta the amoebocytes endeavour to make their way out. This in the star-fish they effect by accumulating at the base of the dermal branchiae and working their way through the thin body-wall and so escaping into the ocean.

Reproductive organs.

The organs of sex in the star-fish are very simple. Both kinds of germ cell are aggregated in great feather-shaped glands situated in pairs in the bases of the arms and opening in the angles between the arms or in the interradii. The ten ovaries in the female and ten testes in the male are connected by a circular cord of immature germ cells called the genital rachis running round the disc just dorsal to the coelom. This is embedded in the wall of a tube called the aboral sinus which like the other spaces in a star-fish, apart from those of the digestive canal, is an outgrowth of the coelom. The rachis is in turn

connected with a pillar of similar cells running alongside the stone-canal which used to be called the heart, under a mistaken idea of its function, but which we shall term the genital stolon. The genital rachis is formed as an outgrowth from the genital stolon and the latter is an outgrowth from the coelomic wall, so that the genital cells are derived from the coelomic cells as in other Coelomata. The genital stolon is interposed between the general coelomic cavity of the animal and a special division of the same which is called the axial sinus, and which runs parallel to the stone-canal. The axial sinus is derived from the anterior portion of the coelom in the larva. Underneath the madreporite there is still another division of the coelom completely shut off from the rest, which may be termed the madreporic vesicle. It seems to be derived from a sac in the larva which is contractile; it possibly represents the pericardium of *Balanoglossus* (see p. 389). The genital stolon projects into the axial sinus; it has a brown colour which no doubt suggested the connection with the blood-system to the earlier anatomists, but true blood-vessels do not exist in Echinodermata. The ova and spermatozoa are thrown out into the water by pores situated on the under or oral surface at the base of the arms and unite with each other there. The young lead a free-swimming existence, and are so unlike the star-fish that no one would ever dream of suspecting that the two had anything to do with each other. As however these peculiarities are fundamentally the same in each of the groups of the Echinoderms they will be dealt with later when the characters of these other groups have been studied.

The other species of star-fish, which are all grouped together in the class Asteroidea (Gr. ἀστήρ, a star; εἶδος, shape), differ but little in really fundamental points from *Asterias rubens.* Pedicellariae may, as we have seen, be absent; the arms may be short so that the shape almost becomes that of a pentagon and the arrangement of the plates and spines constituting the skeleton may vary very much. In one family, the Astropectinidae, there is no anus, the rectum ending blindly, and the tube-feet have pointed ends. These star-fish do not climb but run over the surface of the sand.

The number of arms is most often five, but not only do individual variations from this rule occur in species where five is the normal number, but species and even genera and families are characterised by having a larger number: the common Sun-star, *Solaster papposus*, for instance, has from eleven to thirteen arms.

Class II. Ophiuroidea.

The next order of Echinoderms is termed the Ophiuroidea (Gr. ὀφίουρος, serpent-tailed; εἶδος, form) or the Brittle-stars. These like the star-fish have a body with five arms diverging from a central disc on all sides like the conventional representation of a star. The

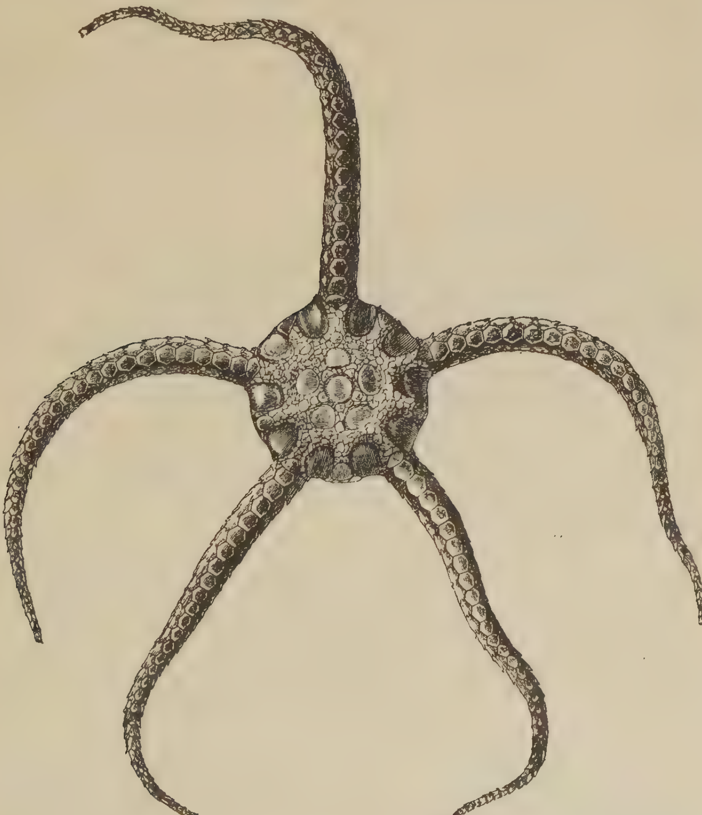

Fig. 155. Dorsal, upper or aboral view of *Ophioglypha bullata* × about 2½. From Wyville Thompson.

arms are, however, sharply marked off from the central disc, and they do not, as in the true star-fish, insensibly merge into it, but are continued along grooves on the under surface to the immediate neighbourhood of the mouth: further they are exceedingly long and flexible and totally unlike the stiff arms of *Asterias* or its allies.

The habits of the animal too are very different from those of the star-fish. Instead of creeping slowly along by the action of the tube-feet it springs along by muscular jerks of the arms, sometimes pushing with four arms and seizing hold in front with one, sometimes pushing with three and hauling itself along with two. The name Brittle-star is derived from the readiness with which, if irritated, the animal will snap off an arm.

As might naturally be expected, the most striking differences from the star-fish are seen in the arms. No ambulacral groove is apparent: the arm is encased in a cuirass consisting of four series of plates, an upper row, two lateral rows each bearing a row

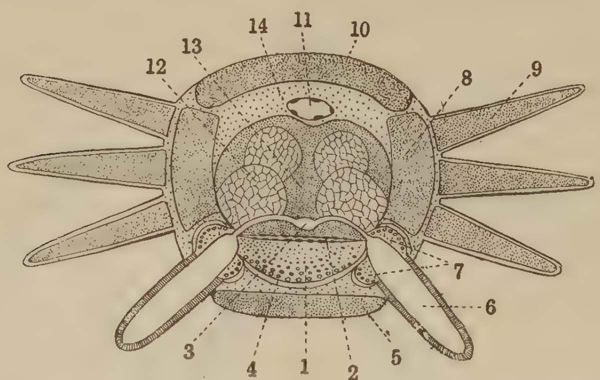

Fig. 156. Section through an arm of an *Ophiuroid*. Diagrammatic, magnified.

1. Radial nerve-cord. 2. Radial perihaemal canal. 3. Radial water-vascular canal. 4. Epineural canal. 5. Ventral plate. 6. Tube-foot. 7. Pedal ganglion. 8. Lateral plate. 9. Spine. 10. Dorsal plate. 11. Coelom. 12. Longitudinal muscle. 13. "Vertebra." 14. Soft tissue supporting plates.

of spines on its edge, and an under row (Fig. 156). On close inspection the short pointed tube-feet may be seen protruding from minute pores at the sides of the under row of plates. A thin section of the arm reveals the fact that there really is a space corresponding to the ambulacral groove of the star-fish, but that by the approximation of its edges it has become closed off from the outer world so that it forms a canal, the so-called epineural canal (4, Fig. 156). Above this canal, at the spot one would term the apex of the ambulacral groove in a star-fish, there is a ridge of nervous matter covered on the lower side by cells exactly resembling the skin cells covering the nerve ridges in *Asterias*. This is the radial

nerve, and above this again is a large rounded disc of calcareous matter, the so-called vertebra. This really corresponds to a pair of ambulacral plates which have become fused together. So much might be inferred from the fact that the radial water-tube runs in a groove on its under surface, and it is clearly proved by examining young specimens. Each vertebra is very short, and it not only has rounded knobs and cups in order to enable it to slide on its successor and predecessor, but is connected to each of them by four great muscles, by the contraction of which the arm is moved in any direction (Fig. 156). If the two side muscles contract the arm is moved towards that side, if the two upper, upwards, and so on.

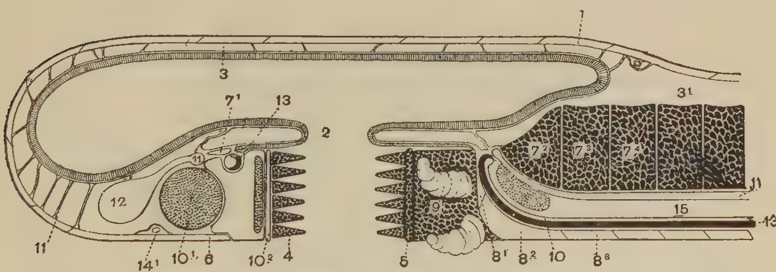

FIG. 157. A diagrammatic vertical section of an *Ophiuroid*. After Ludwig. The circumoral systems of organs are seen to the left, cut across, their radial prolongations cut longitudinally, to the right.

1. Body-wall. 2. Mouth. 3. Coelom. 3^1. Coelom of the arm. 4. Mouth papillae. 5. Torus angularis. 6. Oral plate. 7^1. 1st ambulacral ossicle. 7^2, 7^3, 7^4. 2nd to 4th ambulacral ossicle or "vertebrae." 8^1, 8^2, 8^3. 1st to 3rd ventral plate. 9. 1st oral foot. 10. Transverse muscle of the 2nd joint. 10^1. External interradial muscle. 10^2. Internal interradial muscle. (The line should point to the dotted tissue.) 11. Water-vascular system: to the left the circumoral ring, to the right the radial vessel. 12. Polian vesicle. 13. Nerve-ring and radial nerve: the ganglia on the latter are not shown. 14^1. Genital rachis lying in the aboral sinus. 15. Radial perihaemal canal.

These muscles are the seat of the chief activities of the animal, and it is not surprising to find that a pair of large nerves comes off between each two vertebrae to supply them, and that where these nerves are given off the nerve-cord is thickened and the nerve-cells increased, so that a string of ganglia is produced strongly recalling the ventral nerve-cord of the Earthworm. Between the vertebrae and the radial nerve-cord there is a single canal (2, Fig. 156), representing the pair of radial perihaemal canals in a similar position in Asteroidea. From the ventral wall of this canal the coelomic nervous system is formed: and it is by the greater development of this system where the nerves to the ambulacral muscles are given

off that the ganglionic swellings of the nerve-cord are produced. The vertebrae and these muscles nearly completely fill the arm, leaving only a small canal above the vertebrae (11, Fig. 156): this is an outgrowth of the body-cavity or coelom, but there is no branch of the alimentary canal continued into it, as was the case with the star-fish.

The digestive sac is here a simple flattened bag lined by cells somewhat like those lining the pyloric sac of the star-fish. There is no anus, and the edges of the stomach cannot be pushed out. How then, it may be asked, does the Brittle-star eat and of what does its food consist?

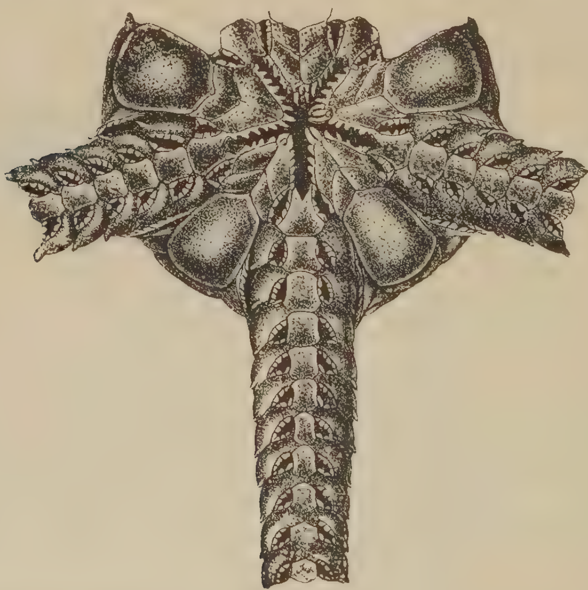

FIG. 158. Oral view of part of the disc and arms of *Ophioglypha bullata* $\times 4\frac{1}{2}$. From Wyville Thompson.

It must be confessed that, in spite of their quick movements and highly developed nervous system, Brittle-stars belong in general to the great army of mud-eaters and scavengers. Where they live—usually at the bottom of sea pools and at such depths of the ocean as to be in still water—the mud or sand is impregnated with decaying animal and vegetable matter, and most Brittle-stars shovel this material into their mouths by means of the two pairs of tube-feet of each arm which lie nearest the mouth and are called the

oral tube-feet. The interradii between the arms project inwards over the mouth, as the mouth-angles; these are lined along their edges and at their tips with broad blunt spines called teeth and mouth papillae, so that they form an efficient strainer and prevent coarse particles entering the stomach (Figs. 158 and 159). The calcareous plate at the apex of each mouth-angle which bears these spines is called the torus angularis (5, Fig. 157). Some Brittle-stars belonging to the genus shown in Fig. 158 have been observed to seize worms by coiling their arms around them and then to devour them.

We saw that in the star-fish the whole surface is covered with a sensitive skin, but that the tube-feet act as sense-organs as well as being locomotor in function. In the Brittle-stars the sole purpose of the tube-feet is to serve as sense-organs; they are often covered with little warts consisting mainly of sense-cells with their delicate hairs sticking out all round, just like the batteries of cnidoblasts in *Hydra*, and in all cases there is a special nervous swelling surrounding the base of each tube-foot called the pedal ganglion (7, Fig. 156). As, however, these tube-feet have lost their power of attaching themselves by a sucking action to objects and hence are of no use for locomotion, the ampullae have disappeared; and as the action of the ampullae is probably the chief cause of the loss of fluid in the tube-feet of the star-fish, in the Brittle-star, where the loss must be very small, the stone-canal is excessively narrow and the madreporite instead of being a regular sieve has two pores only, rarely more. It is very curious to find that the madreporite is on the under side of the animal; in the young Brittle-star it is on the edge of the disc, but in each interradius the upper surface grows more rapidly than the ventral and so it is forced round on to the under-side. To the water-vascular ring are attached four large Polian vesicles, the interradius occupied by the stone-canal alone being without one. The tube-feet are the only sense-organs; this is more exclusively true than is the case with star-fish, for in the Ophiuroidea the rest of the ectoderm, after having given rise to a cuticle, has disappeared, since the solid mail of plates which the animal possesses appears to render it impervious to sensations of contact.

The organs of sex are very simple; they are situated in the disc in the interradii and consist, in each interradius, of several short pouches. These open into ten sacs, called the genital bursae; one pair being placed in each interradius. These sacs are merely invaginations of the ectoderm which does not here disappear as

over the rest of the body; they are lined by ciliated cells which keep up a constant current of fresh water pouring into them and thus they fulfil the same function as the "dermal branchiae" of star-fishes.

Class III. Echinoidea.

The general appearance of the dried skeleton of a Sea-urchin or Echinoid is familiar to most people, but many would fail to

Fig. 159. *Strongylocentrus dröbachiensis* × 1. Aboral surface. From Agassiz.
1. Expanded tube-feet. 2. Spines.

recognise any resemblance to a star-fish in the slightly flattened sphere covered with spines. If, however, we are fortunate enough to see one living, we at once perceive that along five meridians, the sphere is beset with beautiful semi-transparent tube-feet, ending in suckers, exactly like those of the star-fish. In fact, the Sea-urchin

might be described as a star-fish in which the upper surface had shrunk to insignificant proportions, being represented by a small patch of leathery skin at the upper pole: or, if we regard the whole radial tube with its tube-feet as one immense branched tentacle and the arm as its support, we should say that the arm had been again merged in the body so that the radial tube was bent back in a curved course. As a matter of fact the end of the radial tube

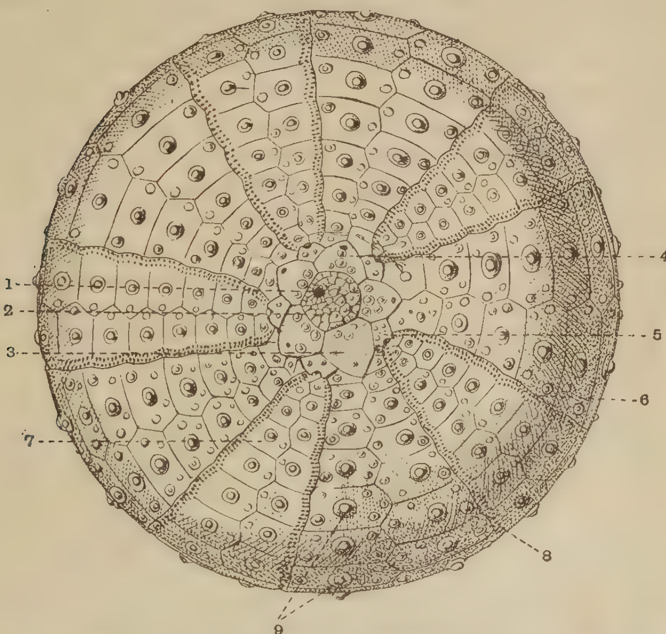

FIG. 160. Diagram of an aboral view of the dried shell of an Echinoid × 1. The spines, pedicellariae and tube-feet have been removed.

1. Anus. 2. Leathery skin round anus, periproct. 3. Madreporic plate. 4. Genital plate with genital pore. 5. Ocular plate with eye. 6. Line of junction of ambulacral and interambulacral plates. 7. Ambulacrum. 8. Pores through which tube-feet protrude. 9. Bosses which bear the spines.

projects very slightly beyond the general surface and bears at its tip a mass of pigment which corresponds with the eye of the star-fish, though no eye-structure has been detected in it. This is situated near the upper end of the body, just outside the small area of leathery skin mentioned above.

The skeleton of the Sea-urchin is a cuirass of plates fitting edge to edge, with two openings. Of these the upper (already referred

to) is covered with leathery skin and has the small anus in the centre of it and is called the periproct (Fig. 167): it is this area which corresponds to the whole upper surface of the star-fish. The other opening is in the centre of the lower surface and is likewise covered by flexible skin; it surrounds the mouth and is called the peristome (Fig. 166).

The cuirass itself is called the corona and consists of twenty strips, each made up of a row of plates. Corresponding to each tube-foot area or radius there are two rows of so-called ambulacral plates, and each intervening area or interradius is similarly covered by two rows of large plates. As in Ophiuroids, there is no ambulacral groove visible from the outside: it is represented by the epineural canal, immediately inside which there is the radial nerve-cord. It is necessary to bear this in mind when the term ambulacral plate is used; the so-called ambulacral plates of an Urchin do not correspond to the similarly named plates in the star-fish, as they do not roof in the ambulacral groove, but form a floor for it. Inside the nerve-cord there is a single radial perihaemal canal as in the Brittle-star (2, Fig. 164 B). As the plates of the skeleton are not movable on one another nothing corresponding to the ambulacral muscles of the star-fish exists, at least over most of the radius, and the radial perihaemal canal is separated from the general coelom only by a thin septum in which the radial water-tube is embedded. For the same reason there is no recognisable coelomic nervous system.

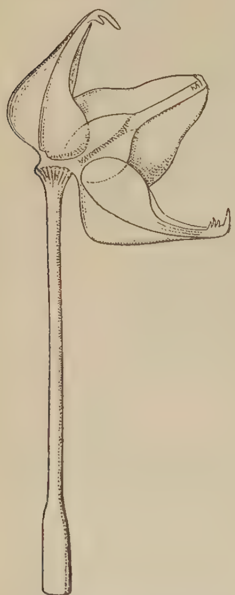

FIG. 161. A glandular or gemmiform pedicellaria from *E. esculentus* × 18. From Chadwick.

If the continuous cuirass of the Sea-urchin and the closed ambulacral groove remind one of an Ophiuroid, the resemblance ends there; for in the Urchin the ectoderm, consisting of long slender cells with a tangle of nerve-fibres at the base, is spread over the whole surface outside the skeleton, just as in a star-fish. This sensitive layer controls, it is found, the movements of the spines, which are among the most important organs of the Urchin. These spines, unlike the spines of the star-fish or Brittle-star, have hollow bases, which articulate with

smooth rounded bosses on the plates (9, Fig. 160, 8, Fig. 164 B). They are tied to these bosses by a sheath of muscle-fibres, so that by the special contraction of any side of the sheath they can be

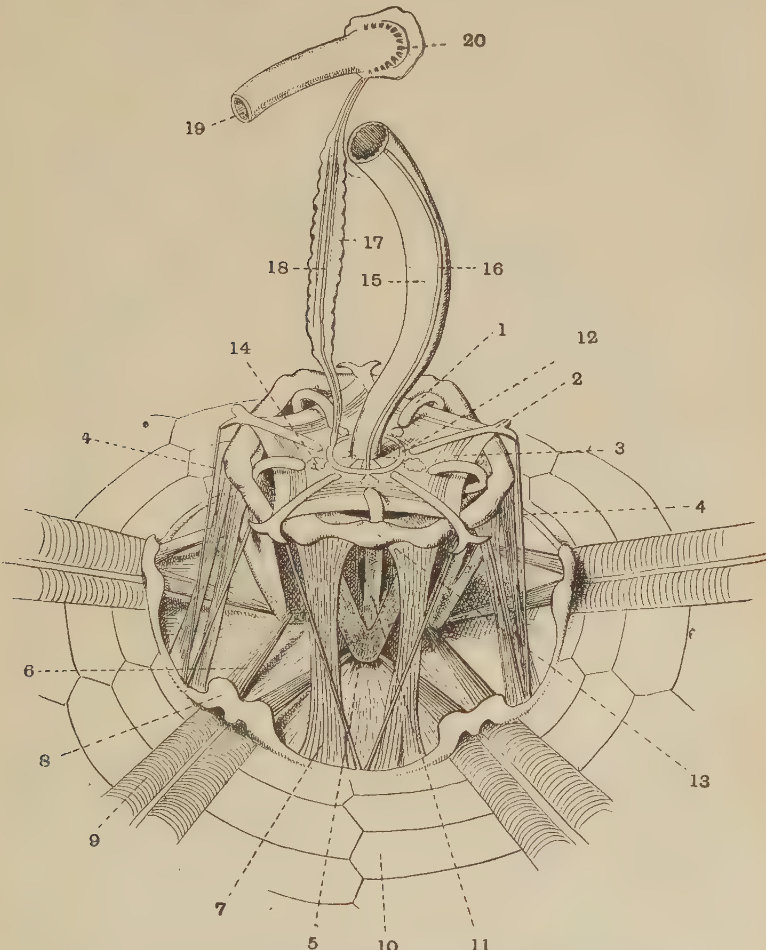

FIG. 162. Aristotle's Lantern of *E. esculentus* × 2. Partly from Chadwick.

1. Upper end of tooth enveloped in lantern membrane. 2. Compass. 3. Elevator muscle of compasses. 4. Depressor muscles of compass. 5. Jaw. 6. Retractor muscles of the jaws. 7. Protractor of jaws. 8. Auricula. 9. Ampullae of tube-feet. 10. Inter-ambulacral plate. 11. Tooth. 12. Circular water-vascular vessel. 13. Epiphysis. 14. Polian vesicles. 15. Oesophagus. 16. Ventral "blood"-vessel. 17. Genital stolon. 18. Stone-canal. 19. Rectum. 20. Madreporic plate.

moved in any direction. The skin covering the sheath has developed a specially thick nervous layer.

Sea-urchins such as we have been describing live on stony or rocky bottoms, over which they slowly creep by means of their tube-feet. The spines are pressed against the substratum and keep the animal from rolling over under the pull of the tube-feet and also help to push it on. The spines are usually of two distinct sizes, longer primary spines, and shorter secondary

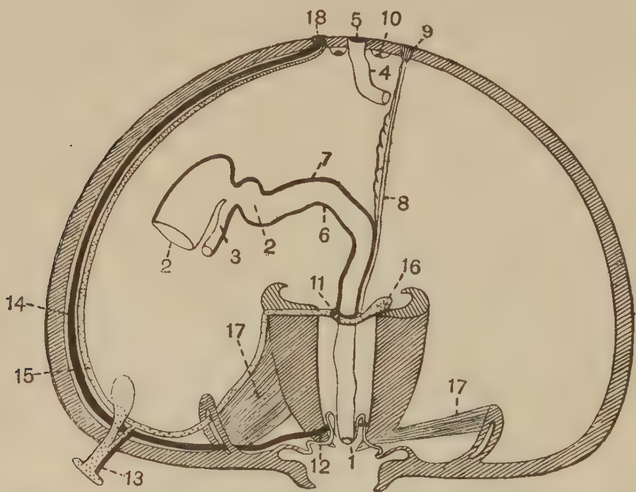

FIG. 163. Diagrammatic vertical section of a Sea-urchin. From Leuckart, after Hamann.

1. Mouth. 2. Intestine cut short. 3. Siphon. 4. Rectum. 5. Anus. 6. Ventral "blood"-vessel on intestine. 7. Dorsal "blood"-vessel on intestine. 8. Stone-canal. 9. Madreporic plate. 10. Genital rachis. 11. Water-vascular ring. 12. Nerve-ring. 13. Tube-foot with ampulla. 14. Radial nerve. 15. Radial water-vessel. 16. Polian vesicle. 17. Muscles; those on the left pull Aristotle's Lantern outwards, those on the right retract it. 18. Ocular plate.

spines. The forest of spines has a kind of undergrowth of pedicellariae. These are of several kinds and are much more highly finished organs than those of star-fishes; they have a long stalk, which is partly stiffened by a delicate calcareous rod, and the jaws are three in number. One kind has short stumpy jaws, each with a poison bag at its base and a stiff stalk; these are doubtless weapons of defence and enable the Urchin to give any unwelcome visitor which may come too close a warm reception. Such pedicellariae are called gemmiform (Fig. 161). Another

kind, termed tridactyle, has long jaws and a flexible stalk. It was supposed that these helped the animal to climb by seizing hold of waving fronds of seaweed till the tube-feet could get a hold, but this is proved not to be the case. It has been shown that a gentle movement in the water excites the tridactyle pedicellariae while a stronger movement calls the gemmiform into activity. The most probable use of the tridactyle pedicellariae is to destroy minute organisms (often the larvae of sessile animals) which would either attach themselves to the skin of the Urchin or burrow into it. Besides these there are two other kinds of pedicellariae. In one of these the so-called "snake-headed" or ophicephalous pedicellariae, the jaws are broad and fringed at the edges with powerful teeth. They articulate with one another at their bases by means of stout semicircular hoops which fit inside one another. This arrangement gives to the jaws a firm grip and this kind of pedicellaria which is scattered all over the surface of the Sea-urchin and is especially abundant on the peristome is the only kind which has been observed to seize and hold small animals such as shrimps which accidentally brush against the Sea-urchin. These are held till the tube-feet can be brought into play, when they are carried round to the mouth and devoured. The last kind of pedicellariae which the Urchin possesses are the most minute of all. They are termed trifoliate pedicellariae; each possesses three blades much broader at the free end than at the base—of the shape in fact which is termed by botanists *obovate.* Two of these blades can seize an object whilst the third blade strikes it. The object of the trifoliate pedicellariae is to free the delicate skin of the Urchin from the sediment which falls on it from turbid water. The lumps of this sediment are broken into the finest dust by these pedicellariae, and this dust is then swept off by the cilia covering the skin.

The Urchin is provided with five white chisel-like teeth, each of which is firmly gripped by a pair of grooved pieces called alveoli, meeting in a point below. Each pair of alveoli meet in a point where they clasp the tooth. Above they are united by two pieces called epiphyses (13, Fig. 162) which meet in an arch. A pair of alveoli with their epiphyses are often spoken of as a jaw, and adjacent jaws are joined by stout, inwardly projecting rods called rotulae. The whole apparatus of five jaws has received the name of "Aristotle's Lantern." This can be pushed out or pulled in by muscles attached to arches called auriculae, rising from the

inner side of the skeleton (8, Fig. 162). Through the auriculae the radial water-tube and nerve pass, and thus they correspond in position to the ambulacral plates of star-fish.

The food of the Urchin consists ordinarily of seaweed which it gnaws with its teeth. No doubt the little worms and molluscs always found in abundance on the surface of the weed add a flavour to the repast and as we have seen it can devour small animals which happen to be caught by its ophicephalous pedicellariae. The alimentary canal is exceedingly unlike those of the Echinoderms so far studied. The gullet ascends vertically between the teeth and passes into the intestinal tube which runs in a spiral right round the body and then turns sharply back and describes one turn of a spiral in the opposite direction, after which it bends inwards and runs straight up to the anus (Fig. 165). For the first part of its course a small tube, the so-called siphon, runs parallel to it, opening into it at both ends.

The water-vascular ring is situated above the masticatory apparatus and is thus widely separated from the nerve-ring, which is situated below it: the radial tubes, in consequence, run downwards along the "lantern" before bending outwards under the auriculae (see Fig. 163). The water-vascular ring bears small pouches which have been termed Polian vesicles. They seem, however, to correspond to Tiedemann's bodies in an Asteroid. The first pair of tube-feet in each radius are different from the rest, in that they are short and not capable of extension, and that their discs are oval. These tube-feet protrude through the peristome and are called the buccal tube-feet; they function as tasting organs, and are thrown into violent excitement if a piece of edible matter is put near them (Fig. 166).

In describing the Asteroidea it was mentioned that the genital stolon or "dorsal organ" had been mistaken by former authors for a heart, and that true blood-vessels were unknown amongst Echinodermata. If by blood-vessel is meant a tube with well-defined walls in which there is a definite circulation of fluid this is strictly true.

It must be remembered, as was pointed out in the chapter on Arthropoda, that blood-vessels and connective tissue have been derived from the same primitive tissue, which may be compared to the jelly of Coelenterata. Now Echinodermata probably represent a stage before the evolution of either blood-vessels or proper connective tissue. Apart from the plates of the skeleton the substance of the

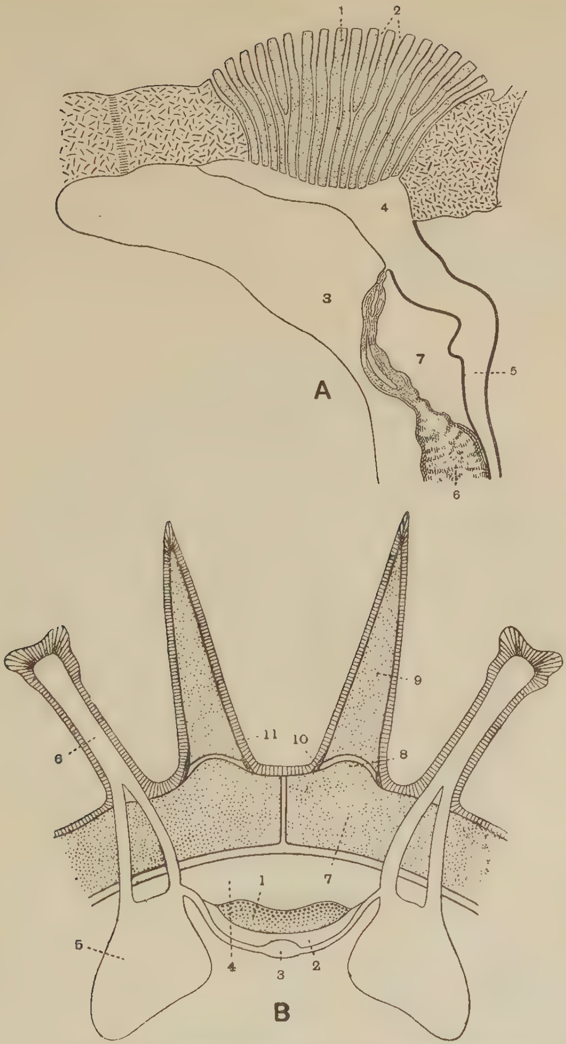

FIG. 164. Sections through parts of *Echinus esculentus*.

A. A section at right angles to the plane of the madreporic plate × 16. From Chadwick. 1. Madreporic plate. 2. Pores in the same. 3. Madreporic vesicle. 4. Ampulla of madreporic plate or dilatation of stone-canal into which the pores open. 5. Madreporic tube. 6. Genital stolon. 7. Axial sinus.

B. A section at right angles to an ambulacral area. 1. Radial nerve-cord. 2. Radial perihaemal canal. 3. Radial water-canal. 4. Epineural canal. 5. Ampulla. 6. Cavity of tube-foot. 7. Ambulacral plate. 8. Boss for articulation of spine. 9. Spine. 10. Muscles which move the spine. 11. Ectoderm.

body-wall has little more consistence than the jelly of an *Aurelia*, and readily degenerates into slime. The ground substance has remained so fluid that it is still traversed by amoebocytes which carry excreta to the interior. In Echinoidea along two tracts, one situated on the same side of the oesophagus as the stone-canal and the other on the opposite side, the jelly intervening between the inner wall of the coelom and the oesophagus has undergone the first stage in the change to a blood-vessel. The fibres are scantily developed and the amoebocytes are present in immense numbers,

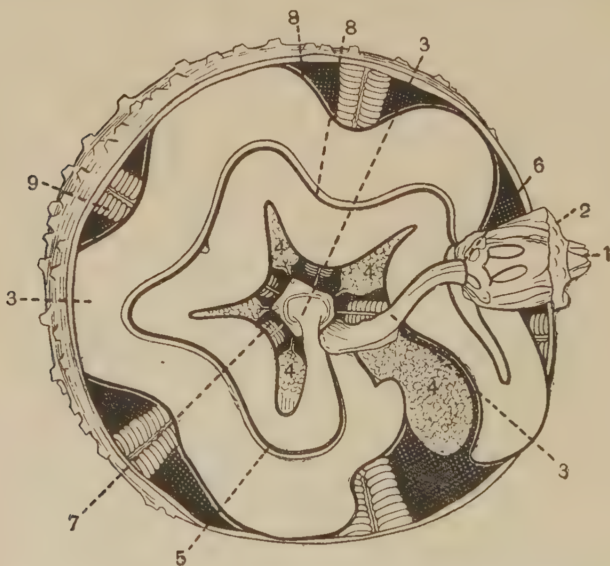

FIG. 165. View of Sea-urchin, with part of the shell removed to show the course of the alimentary canal. From Leuckart, after Cuvier.

1. Mouth surrounded by five teeth (displaced). 2. Lantern of Aristotle. 3. Oesophagus, coiled intestine and rectum. 4. Ovaries with oviducts. 5. The siphon. 6. "Blood"-ring. 7. Fold of peritoneum supporting genital rachis. 8. "Blood"-vessel accompanying intestine. 9. Ampullae at base of tube-feet.

whilst the ground substance has become more fluid and probably contains proteids, since it stains with carmine like protoplasm. These tracts are termed dorsal and ventral "blood"-vessels. The dorsal vessel is on the side next the stone-canal. These tracts have not the form of tubes, but are networks of irregular passages devoid of proper walls. They accompany the alimentary canal throughout most of its course and it seems as if the products

of digestion were accumulated in them. A so-called "blood-ring" of similar character surrounds the oesophagus just above the water vascular ring and into this the two "vessels" open. A similar ring has been described in Asteroidea and Ophiuroidea: in some species of the former class a tract of similar substance appears to run down the arm just above the nerve-cord in the septum separating the two perihaemal canals, and the name of these canals (Gr. περί, around; αἷμα, blood) has been suggested by this circumstance.

Breathing, as one might expect, is carried out wherever the body-wall is thin enough to allow the oxygen to diffuse through,

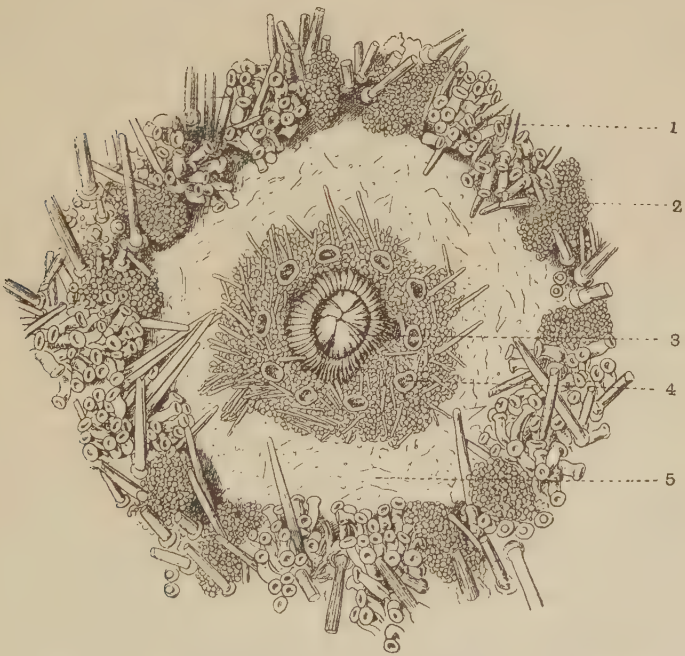

Fig. 166. Oral field of *Echinus esculentus*. Magnified. From Kükenthal.
1. Ambulacrum with tube-feet and spines. 2. Gill. 3. Teeth of Aristotle's Lantern. 4. Buccal tube-feet. 5. Soft membrane around mouth, the peristome.

that is to say by the tube-feet and by the peristomal membrane. The tube-feet, as in the star-fish, are provided with large ampullae which project freely into the great spacious body-cavity. Oxygen thus taken into the fluid filling the tube-feet can be passed into the body-cavity through the ampullae, and there is a curious arrangement to facilitate this. Where the tube-foot passes through the

skeleton it is split into two parallel tubes which reunite below (B, Fig. 164): so that on the dried shell we see on the ambulacral plate several pairs of pores, each pair corresponding to a single tube-foot. As the cells lining the inside of the latter are ciliated, the splitting of the tube is apparently for the purpose of facilitating the separation of the upward and downward currents of water.

The peristome has ten branched pouches, situated one pair in each interradius and projecting outwards. These are the gills, but it is unreasonable to suppose that all the breathing is done by them. They communicate not with the general body-cavity, but with a part of it, called the lantern coelom, shut off from the rest by a septum stretched between the teeth and jaws. Embedded in the upper wall of this are certain rods called compasses, which are connected with each other and with the auriculae by muscles, and by means of these the upper wall of the lantern coelom can be raised or depressed and the pressure inside altered. When these rods are depressed water is driven out into the gills and there absorbs oxygen. When they are raised the water is sucked back into the lantern coelom and the oxygen passes through the thin wall of the latter into the general coelom. A very curious use of the jaws and teeth has recently been demonstrated by Dr Gemmill. When the urchin gets into shallow water and is partly left dry by the tide, then a peculiar rhythmic action is set up in the teeth. The whole lantern is swung forward by the pull of the muscles attaching it to the auriculae. Then the teeth are protruded by the action of the protractor muscles and firmly inserted in the ground, and using the protruded teeth as a fulcrum or as the point of a vaulting pole the body of the urchin tumbles forward. The teeth are then retracted, the lantern is again swung forward and the action is repeated, and in this way the urchin progresses by a series of short leaps. When once this action has been set up it continues for some time after the urchin has been covered with water.

The organs of sex are alike in external appearance in both sexes (Fig. 165). They have the form of five great bunches of tubes hanging down into the body-cavity and opening by five small holes placed in plates called the genital plates, forming the summit of the interambulacral series on the corona and situated just outside the periproct (Figs. 160 and 167). In the young Sea-urchin there is a genital rachis connecting them together, and throughout life there is a genital stolon alongside the stone-canal. The genital stolon is relatively much larger in Echinoidea than in Asteroidea, and

surrounds the axial sinus in the lower part of its course, so that this space appears like a cavity excavated in the stolon. Hence by one author the axial sinus and stolon were mistakenly described as a kidney with glandular walls, and the madreporic vesicle, which is here much enlarged and extends parallel with the axial sinus, was called by the same author the "accessory kidney."

The Echinoidea are divided into three orders:

I. The ordinary Sea-urchins, such as we have described, constitute the order ENDOCYCLICA, which live chiefly on rocky and stony ground. The other two orders live in sand or mud and have under-

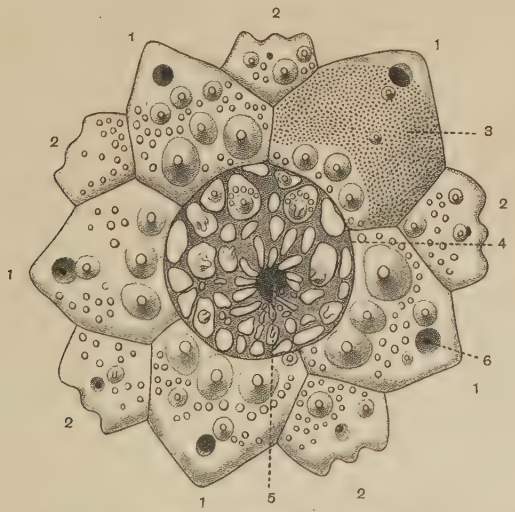

FIG. 167. Aboral system of plates of *Echinus esculentus* × 4. From Chadwick.
1. Genital plate. 2. First plate in the radius pierced for the eye-spot. 3. Madreporite. 4. Periproct, or region round anus. 5. Anus. 6. Genital pore.

gone singular modifications in order to fit them for this kind of life. They are termed the Irregular or Exocyclic Sea-urchins, because whereas the anus has become shifted from the upper pole of the body down one side to the edge, or even to the under surface of the more or less flattened body, the madreporite and genital plates still retain their position. In both orders the tube-feet of the upper part of the ambulacra are the main breathing organs, and are greatly flattened and expanded at the base, while the pores through which they pass are arranged in two converging curves on each ambulacrum, the figure produced being compared to a petal of a

flower, hence the name applied to them, viz. petaloid ambulacra. The special characters of these two orders are as follows:

II. CLYPEASTROIDEA or Cake-urchins. They live at or near the surface of the sand. They still retain their teeth, which are placed almost horizontally, and they use them as spades to shovel the sand into the mouth. All the spines covering the upper surface are ciliated and so a constant current of water sweeps over the expanded tube-feet which act as gills. In addition to these tube-feet the whole aboral surface, radii and interradii included, is covered with a multitude of minute tube-feet provided with suckers. Similar tube-feet are found on the oral surface, but they are confined to the radii. This immense multiplication of tube-feet is of course due to the small purchase that any one of them is able to get on such a yielding material as sand. In a word, the animal moves itself by a multitude of minute pulls instead of by a lesser number of stronger pulls as do the Endocyclica. There are calcareous pillars stretching from the upper to the lower surface of the shell or test, apparently to enable them to withstand rough usage, since in many cases they live within reach of the breakers. The best known British species is *Echinocyamus pusillus*, a little oval Sea-urchin about the size of a pea, whence the common name applied to it, viz. Pea-urchin. On the east coast of North America one species, *Echinarachnius parma*, the Sand-dollar, is very common; this is an extremely flattened urchin of circular outline, the shape and size of which have suggested a comparison with the famous silver-dollar of the United States currency.

III. SPATANGOIDEA or Heart-urchins. These live buried at depths of a few inches to a foot beneath the surface of the mud, and the body is more or less oval or egg-shaped, slightly flattened underneath. The mouth is sometimes in the centre of the under surface and sometimes nearer one end, and is usually crescentic and always without any trace of jaws. These urchins have usually only four of the ambulacra "petaloid"; the fifth has a few long tube-feet with expanded fringed discs. In the case of the familiar British species *Echinocardium cordatum* it is known that the urchin extends these tube-feet from its burrow up to the surface of the sand and collects with them small organisms lying on the surface. These are pushed within reach of the buccal tube-feet and so reach the mouth.

The Spatangoidea do not use their tube-feet to walk with, but move by means of spines which are provided with flattened tips,

and so the small tube-feet present in such multitudes in the Clypeastroidea are absent. Besides these spines they possess peculiar lines of very small spines covered with cilia, which cause a current to pass over the gill-like tube-feet. Such rows of ciliated spines are termed fascioles.

Class IV. Holothuroidea.

The fourth group of the Echinoderms is termed the Holothuroidea or Sea-cucumbers, and consists of animals of a more or less sausage-shaped form, with the mouth at one end and the large anus at the other.

These animals have undergone the same essential modification as the Sea-urchins, the arms having been re-absorbed into the body so that the radial tubes run down the side of the body and end near the anus. The nervous system also is situated beneath the surface, the ambulacral groove being represented by the epineural canal. The skin, as in Echinoidea, retains its well-marked ectoderm with the nervous layer at its base.

They are however distinguished by some most marked characteristics: 1. The skeleton has almost entirely disappeared, being represented only by grains and prickles of various shapes completely buried in the skin. 2. The muscular system of the body-wall is most powerfully developed: there is a pair of strong longitudinal muscles running inside each radial water-tube, and transverse muscles run across each interradius. 3. The buccal tube-feet termed "tentacles" are highly modified and are the means by which the animal feeds itself. 4. The anus is wide and the concluding portion of the intestine termed the cloaca is strongly muscular, and it is used as a breathing organ, water being sucked in at the anus and thrown out again. 5. The stone-canal does not reach the exterior, but terminates in a sieve plate hanging down into the interior of the body.

The breathing by means of the anus is carried out by certain organs called gill-trees. These are two great branched tree-like outgrowths of the hinder part of the intestine, reaching right through the body-cavity to near the mouth (Fig. 168). Water is taken in by the anus and forced up into the finest branches and no doubt diffuses through their walls into the body-cavity under the pressure set up by the contraction of the muscles of the anus. Hence it is that the animal is able to dispense with an external madreporite,

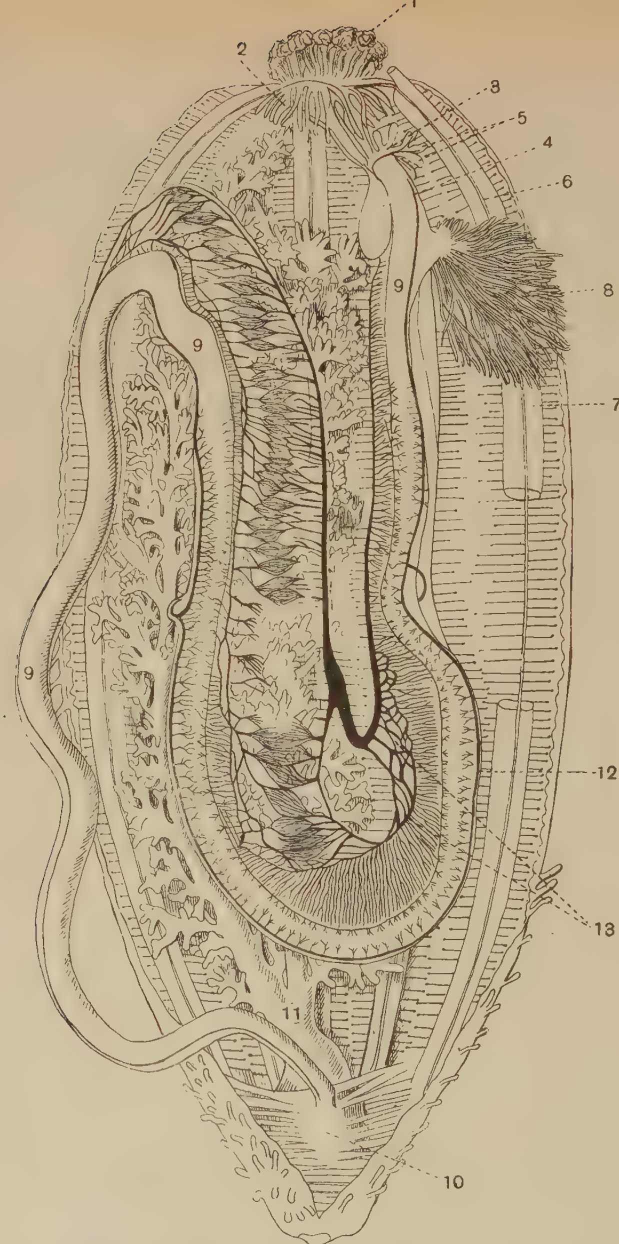

FIG. 168. View of *Holothuria tubulosa* somewhat diminished. The animal is opened along the left dorsal interradius and the viscera are exposed. After Ludwig.

1. Tentacles. 2. Ampullae of tentacles. 3. Water-vascular ring. 4. Polian vesicle. 5. Stone-canals. 6. Radial water-vessel. 7. Radial longitudinal muscle partly cut away. 8. Reproductive organ. 9. Alimentary canal. 10. Cloaca. 11. Respiratory trees. 12. Ventral "blood"-vessel. 13. Dorsal "blood-plexus."

and also to obtain the fluid necessary to keep its tube-feet tense from its own body-cavity. From the water-vascular ring one or more long-stalked Polian vesicles hang down into the body-cavity.

The muscular body-wall has a very curious effect on the economy of the animal. When it is irritated it contracts the muscles, and since the fluid in the body-cavity is practically incompressible, the effect is to set up a tremendous pressure. As a result of this the wall of the intestine near the anus tears and a portion or the whole of the intestine is pushed out. The gill-trees are the first to go, and in some species the lower branches of these are covered with a substance which swells up in sea-water into a mass of tough white threads in which the enemies of the animal are entangled. A lobster has been seen to be rendered perfectly helpless as a consequence of rashly interfering with a Sea-cucumber. These special branches of the gill-trees are termed Cuvierian organs.

A Holothuroid is only temporarily inconvenienced by the loss of its internal organs. After a period of quiescence it is again furnished with the intestine and its appendages. Some species, which are able to pull in the mouth end of the body with the tentacles, when strongly irritated snap off even this, and yet are able to repair the loss.

The intestine is a simple looped tube which has three limbs. One limb runs down towards the anus, the next turns up again towards the mouth and then bends back into the final limb which goes towards the anus. These limbs are attached by mesenteries to different interradii of the body, the first to that which in the ordinary position of the animal is mid-dorsal, the next to the left ventral, and the third to the right ventral (Fig. 168).

Accompanying the alimentary canal are so-called dorsal and ventral "vessels" similar to those of the Echinoidea, and there is also a "blood-ring" like that described in the same class. In Holothuroidea the ventral vessel is close to the alimentary canal but the dorsal vessel is borne on a little ridge projecting from the intestine. The alimentary canal is enswathed by minor branches of the network of which the dorsal and ventral vessels form merely the large trunks. The whole system thus assumes a very complicated appearance, but even here it has been shown that there is no circulation nor even a proper wall to the spaces. The longitudinal vessels indeed often do not appear to communicate with the blood-ring.

The buccal tube-feet form a crown of from ten to twenty-five great branched tentacles, and their different shapes are used to classify the various orders of the Sea-cucumbers. Most species feed on sand or mud, but one order can be described only as anglers. In them the tentacles are long and delicately branched so that they resemble pieces of seaweed. The animal stretches them out, and they become the resting-place of numbers of the minute animals which swarm in sea-water. When one tentacle has got a sufficient freight it is bent round and pushed into the mouth which is closed on it. It is then forcibly drawn out through the closed lips so that all the living cargo is swept off.

The organs of sex are similar in nature to those of the urchins, but are represented by only one mass of tubes which all unite in a common opening near the tentacle region, and it is in this region that the stone-canal opens in the one or two rare cases where it still opens to the exterior. Hence it appears that whereas in the irregular Sea-urchins the genital openings and madreporite have remained fixed while the anus has been shifted, here the anus has remained in its original position while the genital opening has been shifted towards the mouth.

The Holothuroidea are divided into the following six orders:

1. Aspidochirotae: Sea-cucumbers with shield-shaped ends to the tentacles,—these have also large ampullae so that they can be individually retracted. With gill-trees and often Cuvierian organs.

2. Dendrochirotae: Sea-cucumbers with long delicately-branched tentacles without ampullae. The whole front end of the body can be pulled in by means of special muscles. Gill-trees present.

3. Synaptidæ: Sea-cucumbers in which the tentacles have two rows of short branches. No tube-feet except these, the radial canals having also disappeared. No gill-trees. The body-wall is thin and transparent and oxygen can diffuse through it.

4. Molpadidae: Sea-cucumbers with tentacles unbranched or with two or four small lateral branches, and no other tube-feet except a circle of papillae round the anus. Gill-trees present.

5. Elasipoda: Sea-cucumbers whose tentacles have shield-shaped ends drawn out into short processes. No gill-trees. The tube-feet of the upper surface of the body modified into stift respiratory processes. Live only at great depths in the ocean.

6. Pelagothuriidae: Sea-cucumbers which swim or float at the surface of the sea. The buccal tentacles are the only tube-feet

present and they have shield-shaped ends. They have long ampullae which project into a thin web or swimming membrane which surrounds the front part of the body like a collar. No gill-trees. The stone-canal opens on the external surface.

Class V. Crinoidea.

The last group of the Echinoderms is termed the Crinoidea (Gr. κρίνον, a lily), animals long familiar to collectors of fossils under the name of Lily-encrinites. They differ from other Echinoderms in that from the centre of what corresponds to the upper or aboral surface of other orders, there springs a jointed stalk by which the animal is moored to the substratum.

Animals of this type were much more common in past times than now. Large masses of limestone are actually made up of their skeletons. The modern order of Crinoidea includes a few species surviving at great depths in the ocean, and about the mode of life of these we know little. There are, however, besides these a number of species not sharply marked off from each other assigned to a family, the Comatulidae, containing two genera, *Antedon* and *Actinometra*, which live at moderate depths in the ocean and which have been thoroughly studied. These however are exceptional in that they break off from the stalk when they are mature and swim about by muscular movements of the long arms. The stump of the lost stalk forms a knob called the centro-dorsal ossicle, which is provided with grasping processes called cirri, by means of which the animal can temporarily attach itself.

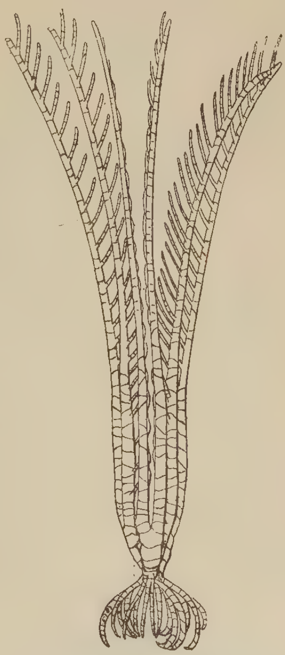

Fig. 169. *Antedon acoela*, Car. A young individual × 1½. After Carpenter.

We may select for our type the common *Antedon rosacea*, which can easily be captured by the dredge at moderate depths. This animal has a small disc and ten extremely long arms. It

reminds one of a star-fish, in the fact that on the oral sides of these arms there are open grooves converging to the mouth, and that the skin lining these grooves is modified to form nervous bands uniting in a ring round the mouth. These ambulacral grooves are further lined by powerful cilia which cause currents of water carrying small animals to flow towards the mouth, and thus the animal is

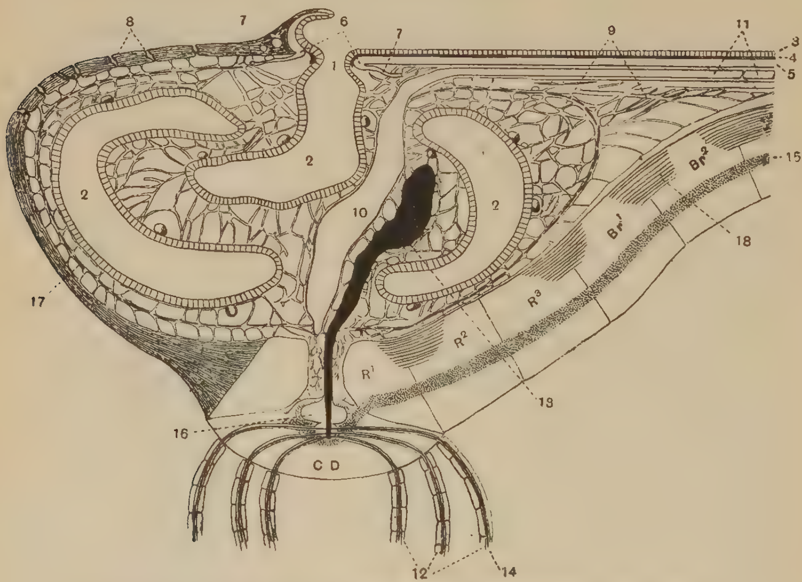

FIG. 170. Transverse section through the disc and base of an arm of *Antedon rosacea.* After Ludwig.

1. Mouth. 2. Various sections of alimentary canal. 3. Epithelium of ambulacral groove. 4. Nervous layer of ambulacral groove. 5. Radial water-canal. 6. Circumoral water-vascular ring. 7. Stone-canals. 8. Pore-canals. 9. Trabeculae traversing the coelom. 10. Axial coelom communicating with 11. 11. Coelom of arm. 12. Cirri. 13. Genital stolon giving off 14. 14. Branches of genital stolon in cirri. 15. Radial nerve of dorsal nervous system. 16. "Chambered organ" in centre of dorsal nervous system. 17. Calcareous rods developing into trabeculae. 18. Muscles connecting radial and brachial plates. CD. Centro-dorsal piece. R^1, R^2, R^3. First, second and third radial plate. Br^1, Br^2. First and second brachial plate.

fed. The tube-feet are small and apparently of use only as gills, those springing from the grooves on the disc alone retaining their sensory function.

The skeleton is peculiar. The ventral side of the body is covered by a leathery skin, but on the aboral side there are first the centro-dorsal ossicle, a round knob representing the uppermost

joint of the stem, and then five rows of plates, called radials, radiating from it. These five rows show us that here, as in most other Echinoderms, we have to do with five primitive arms or radii; these radii, however, bifurcate the moment they become free from the disc, and so there are ten arms: the uppermost plate in each of the five rows having a double facet, on to which fits the lowest of the rows of plates supporting the arms.

The arms really bifurcate again and again, but in each case one of the forks does not develop further and forms a pinnule. If in the case of any of the bifurcations both forks were to develop we should have an increase in the number of arms, and indeed species of *Antedon* with twenty, forty and even one hundred arms are known.

There is no madreporite, but the whole of the upper soft integument is riddled with isolated pores which lead into the body-cavity and are lined by ciliated cells. The water-vascular ring has hanging down from it a large number of stone-canals, which also open freely into the body-cavity. Only one pore and one stone-canal exist in the stalked young, but their position, comparatively near the mouth, is utterly different from that in any other Echinoderm. In the adult the cavity of the coelom is traversed in every direction by cellular cords called trabeculae.

The anus is situated on the ventral side of the body in an interradius, the alimentary canal being coiled in a simple spire in the disc. We have spoken above of the ambulacral grooves being lined by nervous cells, like those forming the radial nerve in star-fish. This is indeed so, but

FIG. 171. *Rhizocrinus*. × about $2\frac{1}{2}$. From Sars.

the Crinoid possesses another and much more important nervous system. From the body-cavity five canals are given off which penetrate the stalk. These canals swell up in the substance of the centro-dorsal ossicle into chambers, and in the permanently stalked forms like *Rhizocrinus* or *Pentacrinus* they form similar chambers wherever the stalk bears cirri. The coelomic cells which form the walls of these canals develop great masses of nervous fibrillae. In *Antedon* of course only the five uppermost chambers remain when the stalk disappears—they are termed collectively the chambered organ—and the nervous lining of these constitutes a kind of brain (Fig. 170). This "brain" is separated from the body-cavity of the calyx by a shelf-like fold strengthened by a calcareous plate called the rosette, which represents a circle of five plates alternating with the columns of radials clearly seen in more primitive Crinoids. From this brain cords go off to the cirri, and five great cords run upwards, perforating the radial rows of plates and eventually bifurcating pass into the arms, perforating the plates which form the skeleton of the latter. These cords are at first tubular outgrowths from the brain, the cells forming the walls of which become converted into nervous matter. It has been experimentally proved that it is this nervous system which controls the muscles moving the arms, and that if the whole soft part of the disc including the ambulacral nervous system be removed the animal swims just as well as before.

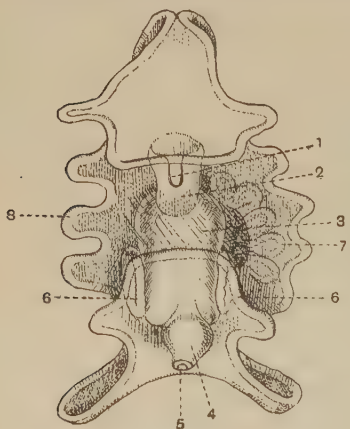

FIG. 172. Ventral view of a larva of a Holothurian taken at Marseilles × about 100. From Joh. Müller.

1. Mouth. 2. Oesophagus.
3. Stomach. 4. Rectum.
5. Anus. 6. Coelomic sac.
7. Rudiment of water-vascular system.
8. Ciliated band.

The organs of sex are rounded masses found in the pinnules and are really, as in Asteroidea, Ophiuroidea and Echinoidea, swellings on branches of a genital rachis. There is also a genital stolon, which however has no connection with any of the stone-canals, but rises from the rachis to the centre of the dorsal wall of the coelom. The young are carried on the pinnules for some time and have a very short free-swimming life, very soon settling

down and developing into little pentacrinoids with a jointed stalk. The name "pentacrinoid" is suggested by their resemblance to *Pentacrinus.* These stalked young present interesting features in the skeleton found in many living and fossil Crinoidea but absent in the adult *Antedon.* Thus the mouth is guarded by five interradial valves each supported by an oral plate, and the rosette is represented by five ossicles.

Leaving aside the Crinoidea, the development of which is known only in one case and is there evidently much modified, the eggs of the other four groups of Echinoderms develop into free-swimming animals which for periods varying from a fortnight to six weeks lead a free life at the surface of the ocean. These young are called Dipleurula larvae and they are, as mentioned, utterly different from adult Echinoderms: unlike these, but like most other animals, they are bilaterally symmetrical (Fig. 172). They swim by means of a powerful longitudinal ciliated ring, drawn out into a number of arms or processes. They possess a complete alimentary canal, consisting of oesophagus, stomach and rectum, while the coelom is represented by two sacs lying one at each side of the digestive tube. These sacs, as a study of the early development teaches, are portions of the alimentary canal budded off from the rest. One of the most interesting features in the development is the fact that these sacs undergo transverse division in the same way as do the mesodermal bands of an Annelid. On the left side three segments are formed, on the right side usually two, but in the Dipleurula larva of Ophiuroids three, of which the middle one has usually a transient existence. The most anterior on each side often coalesce to form a median sac into which the originally single madreporic pore opens on the left side; in the Dipleurula larva of *Asterias* a similar pore is formed on the right side, but this has only a transient existence; a portion of this sac becomes the axial sinus of the adult. The middle section on the left side takes on the form of a curved wreath with five lobes projecting from it; by the union of the two ends of this wreath it is converted into a ring which becomes the future water-vascular ring, whilst the lobes form the radial canals of the adult. This wreath is termed the hydrocoele. The transient middle section of the coelom, on the right side in the larvae of Ophiuroidea, sometimes forms a similar hydrocoele, which is then termed the right hydrocoele, and occasionally a middle section of the coelom is cut off on the right side in the larvae of Asteroidea and Echinoidea.

which also develops into a hydrocoele. The coelom on the right side of the larva of Holothuroidea is not segmented at all. The madreporic vesicle arises as an outgrowth from the most anterior section of the coelom on the right side, very near the mid-dorsal line. The most posterior divisions form the body-cavity of the adult; the left one grows in a ring-shaped manner, encircling, as with a wider ring, the ring of the hydrocoele, while through the centre of both rings the oesophagus of the adult grows. The oesophagus of the larva is usually cast off, but sometimes, as in the Ophiuroidea, it is directly converted into that of the adult by being shifted to the left before the rosette of the water-vascular system becomes a ring.

The Dipleurulae of the Asteroidea fix themselves at the conclusion of their larval life by the anterior end of the body, using the prae-oral lobe as a stalk. The fixed stage is omitted in Ophiuroidea, Echinoidea and Holothuroidea, but the larva of *Antedon rosacea*—the only Crinoid whose development is known—also converts the prae-oral lobe into a stalk. But in the case of the Asteroidea the body becomes bent on the stalk in such a way that the stalk springs from close to the mouth of the adult. The stalk is eventually absorbed and the star-fish commences its adult life, breaks loose from its attachment and moves away. In the Crinoid, on the other hand, the mouth becomes rotated away from the stalk, and the latter seems to spring from the aboral surface.

The whole of this development seems to point to the conclusion that the radially symmetrical Echinodermata are derived from a bilaterally symmetrical ancestor with traces of metameric segmentation; that the acquisition of radial symmetry was due in the first instance to the assumption of a fixed mode of life, followed by the dwindling of the organs of the right side and the compensating greater growth in those of the left. The Crinoidea seem to have retained the original mode of feeding by means of the current produced by cilia, and in them the mouth became shifted upwards away from the stalk into a position favourable for the capture of floating prey. In the Asteroidea and the other Eleutherozoa food is obtained by seizing it with the tube-feet, and hence in these the mouth was bent downwards so that the stalk seems to spring from the oral surface.

This development is not only interesting on account of the extraordinary metamorphosis which the young undergo, but also on account of the fact that whilst the adult is utterly unlike any of the other Coelomata, the structure of the young is reconcilable with the

fundamental structure of Annelida and Mollusca, etc. The only plausible explanation of this is to be found in the hypothesis that the young represent in a rough sort of way the ancestor from which the Echinoderms were derived.

When the Vertebrata are dealt with it will be pointed out that the larvae of the most primitive forms of that group bear a striking resemblance to those of the Echinodermata, and that in the embryos of many Vertebrata the coelom undergoes at first a similar division to that which occurs in the Dipleurula, suggesting the conclusion that the highest groups in the animal kingdom are also sprung from the same ancestor as gave rise to the Echinoderms.

The phylum Echinodermata is classified as follows:

Sub-phylum A. **Pelmatozoa.**

Echinodermata which are fixed to some foreign object during the whole or part of their existence by a jointed stalk springing from the centre of the aboral surface.

Class I. CRINOIDEA.

Pelmatozoa with five long arms which repeatedly fork. The genital organs are borne in the tips of the branches.

Sub-phylum B. **Eleutherozoa.**

Echinodermata which are free during the whole of their adult existence and rarely fixed even during the larval condition. When the immature form is fixed the stalk springs from the oral surface near the mouth and is not jointed.

Class I. ASTEROIDEA.

Eleutherozoa with arms (free radii) containing outgrowths of the alimentary canal and open ambulacral grooves. The arms have feebly developed muscles and locomotion is effected entirely by the tube-feet.

Ex. *Asterias, Echinaster.*

Class II. OPHIUROIDEA.

Eleutherozoa with arms sharply marked off from the central disc. The arms do not contain outgrowths of the alimentary canal and have closed ambulacral grooves. They have highly developed muscles, and locomotion is entirely effected by the arms, the tube-feet being purely tactile.

Ex. *Ophioglypha.*

Class III. Echinoidea.

Eleutherozoa in which the arms have coalesced with the body, the radii being arranged like meridians on a sphere. The ambulacral grooves are closed. The body has a complete armour of closely adjusted plates and the spines are movably articulated with these and assist in locomotion.

Order 1. **Endocyclica.**

Echinoidea in which the anus is in the centre of the aboral pole and teeth are present.

Ex. *Echinus.*

Order 2. **Clypeastroidea.**

Echinoidea in which the anus is excentric, the dorsal tube-feet are flattened and teeth are present.

Ex. *Clypeaster*, *Echinocyamus*, *Echinarachnius.*

Order 3. **Spatangoidea.**

Echinoidea with an excentric anus and flattened dorsal tube-feet but without teeth.

Ex. *Echinocardium.*

Class IV. Holothuroidea.

Eleutherozoa resembling Echinoidea in the coalescence of the arms with the body and in the closed condition of the ambulacral grooves; but with rudimentary skeleton, highly developed muscular body-wall and greatly enlarged buccal tube-feet by means of which all the food is obtained.

Order 1. **Aspidochirotae.**

Buccal tentacles with shield-shaped ends; front part of body not retractile, gill-trees present.

Ex. *Holothuria.*

Order 2. **Dendrochirotae.**

Buccal tentacles branched in tree-like fashion; front part of body retractile, gill-trees present.

Ex. *Cucumaria.*

Order 3. **Synaptidae.**

Buccal tentacles feather-shaped, no other tube-feet; radial canals and gill-trees absent.

Ex. *Synapta.*

Order 4. **Molpadiidae.**

Buccal tentacles small, tube-shaped, unbranched or slightly branched, no other tube-feet; gill-trees and radial canals present.

Ex. *Molpadia.*

Order 5. **Elasipoda.**

Buccal tentacles with shield-shaped ends, body flattened, no gill-trees present.

Ex. *Elpidia.*

Order 6. **Pelagothuriidae.**

Buccal tentacles with shield-shaped ends, and long ampullae projecting into swimming collar; no gill-trees and no other tube-feet.

Ex. *Pelagothuria.*

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CHAPTER XV

PHYLUM BRACHIOPODA

BRACHIOPODS (Gr. βρᾰχίων, the arm; πούς, ποδός, the foot) are true Coelomata and retain the coelom in a primitive and typical condition. Like the Mollusca, they are not segmented, and the only trace of a repetition of parts in the group is in a genus called *Rhynchonella* in which the excretory organs are repeated, so that we find two pairs. A similar repetition of the same organs occurs amongst the Mollusca in *Nautilus*.

External features. Brachiopods are exclusively marine. They have a shell consisting of two valves, so that at first sight they appear to resemble the Pelecypoda, but in Brachiopods the shells are placed ventrally and dorsally, and not on the two sides of the animal as in Pelecypoda. In a few cases such as that of the primitive genus *Lingula* the two valves of the shell are nearly alike in size and shape and consist largely of horny matter or chitin. In most cases however the shell is calcareous, and since in Brachiopoda, as in most bilaterally symmetrical animals, the two sides resemble one another whilst the back and front are unlike, each valve of the shell is symmetrically shaped, but the dorsal valve differs from the ventral, the latter being usually the larger. In a few cases, such as that of *Crania*, a British form common in certain localities, the ventral valve is flat and attached by its whole surface to the substratum; all that is then seen is the arched dorsal valve. Since in the overwhelming majority of Pelecypoda the two valves of the shell are similar in appearance, while each is asymmetrical in shape, the umbo being situated near the anterior end, it is easy to distinguish at a glance the shells of the Pelecypoda from those of the Brachiopoda (Fig. 173).

The posterior end of the body terminates in a stalk which in *Lingula* helps to keep the animal in the holes of the sand in which it lives. In other forms the stalk is shorter and it is firmly glued

to a rock so that when it has once fixed itself a Brachiopod cannot change its place of residence (Fig. 176). Each valve of the shell is lined by the body-wall of the animal, but the body does not occupy the whole of the space between the two valves; it is produced into two folds or flaps called the mantle-folds, which are each hollow and contain extensions of the coelom. These secrete the larger part of the valves of the shell. In *Lingula* and some others the free edges of these mantle-folds, lying parallel with the free edges of the shells, bear a number of chaetae which recall those of the Chaetopoda. It is by no means certain that the shell of Brachiopods is an external secretion like that of Mollusca: it seems possible that it is really deposited in the connective tissue under the ectoderm.

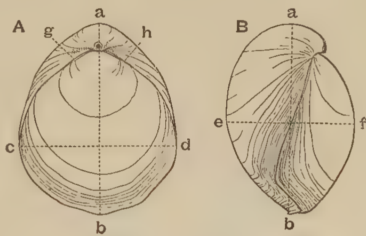

FIG. 173. *Terebratula semiglobosa*, a fossil Brachiopod shell × ⅔.

A. Dorsal view. B. Lateral view. a. posterior, b. anterior end. The line between a and b is called the length, it traverses the aperture through which the stalk projects. The line between c and d is the breadth, between e and f the thickness, and between g and h the hinge-line.

In most of the thick-shelled forms the shell is traversed by processes of the mantle, which nourish it, so that in dried Brachiopods the shell seems perforated with a number of pores.

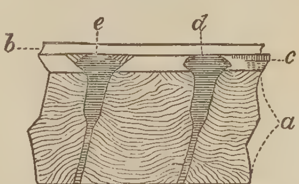

FIG. 174. A section through the shell of *Waldheimia flavescens*. Magnified.

a. Prismatic layer formed in connective tissue. *b.* Epidermal layer. *c.* Outer calcareous layer. *d, e.* The expanded outer ends of the tubes which traverse the shell.

If we open the valves of the shell of a living Brachiopod (slightly so as to avoid tearing the tissues) and look in, we shall see between the ventral and dorsal mantle-folds the anterior body-wall of the creature. This sometimes runs almost horizontally across between the space within the valves, but often slopes obliquely from the ventral to the dorsal valve of the shell. Part of this wall is modified to form two long ridges, the ends of which project freely and are called the arms; they are coiled and are beset with tentacles (Fig. 175). Running close to the origin of the tentacles is a little lip or flange so placed that between it and the tentacle is a groove or gutter. The

groove is lined with cilia and so is the inner face of each tentacle. The whole of this apparatus is called the lophophore. It might be described as a ring of tentacles, the ends of which are drawn out so as to form the arms. It is never quite so simple as the above account would lead one to suppose, for the ring is often produced into two minor lobes forming the lesser arms situated between the main ones, and in many genera the two main arms are raised up from the level of the body-wall and each is twisted into a spiral. The dorsal shell may be prolonged into a series of plates and even into elaborate bands and loops which serve to support such lophophores.

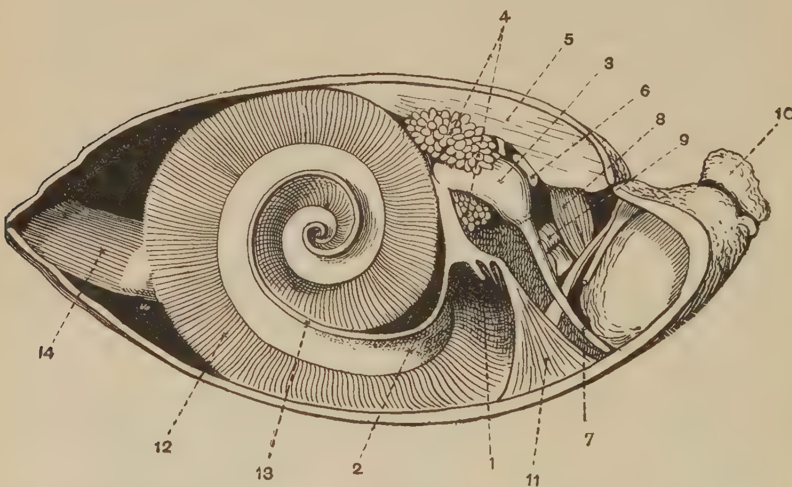

FIG. 175. View of the inner side of the right half of *Waldheimia australis*. From a dissection by J. J. Lister.

1. Mouth. 2. Lophophore. 3. Stomach. 4. Liver tubes. 5. Median ridge on dorsal shell. 6. Heart. 7. Intestine, ending blindly. 8. Muscle from dorsal valve of shell to stalk. 9. Internal funnel-shaped opening of kidney. 10. Stalk. 11. Body-wall. 12. Tentacles. 13. Coil of lip. 14. Terminal tentacles.

Internal structure.

The mouth lies on the middle line at the bottom of the gutter between the lip in front and the tentacles behind. The lophophore is thus an organ for catching food and passing it into the mouth. The cilia which cover the inner surface of the tentacles and line the gutter set up small whirlpools in the water so that minute animals and algae becoming involved in these are swept into the mouth. In many species the

tentacles can be protruded between the valves of the shell, and thus the area they affect is enlarged. The lip may be compared to the epistome of the Phylactolaematous Polyzoa (p. 377).

The mouth leads into a simple stomach which ends in a short intestine. Both stomach and intestine are ciliated. A digestive gland called the liver consisting of a number of branching tubes opens on each side into the stomach, and as is the case in the Crustacea much of the digestion takes place inside these glands. In the genera of Brachiopoda which have a hinged shell the intestine ends blindly, but in those which have no hinge there is an anus which may open in the middle line as in *Crania*, or on the right side of the body as in *Lingula*.

On the dorsal surface of the stomach is a small, muscular, contractile vesicle, the heart (Fig. 175). This gives off a number of vessels, amongst others one which passes to each tentacle, an indication that the tentacles have a respiratory function.

The chief part of the nervous system retains its primitive relation to the ectoderm. Just in front and just behind the mouth there are thickenings of the ectoderm forming a supra- and sub-oesophageal ganglion respectively, the latter contrary to the usual rule being much the larger (Fig. 176). They are connected by two lateral cords and give off a number of nerves, one of which runs to each tentacle. No sense-

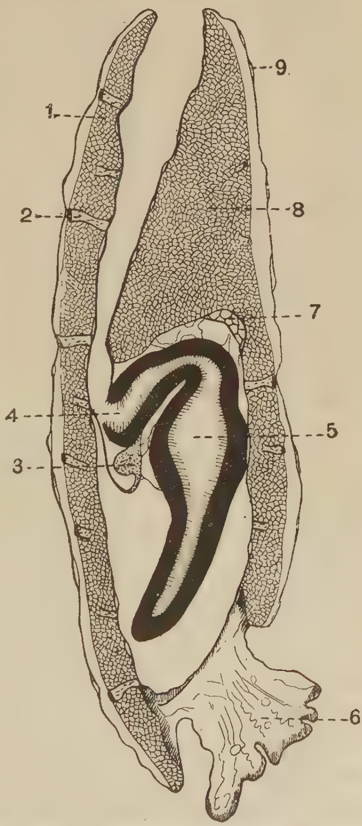

Fig. 176. A longitudinal vertical median section through *Argiope neapolitana*.

1. Ventral shell. 2. Canal containing blood-vessel. 3. Sub-oesophageal nerve-ganglion. 4. Mouth. 5. Stomach. 6. Stalk. 7. Plexus of blood-vessels. 8. Median crest on dorsal shell. 9. Membrane which has separated from shell during the process of decalcification.

organs, such as ears or eyes, are known; and indeed the fixed Brachiopod, whose "strength is to sit still" and sweep little particles of food towards its mouth, has but little need of specialised sense-organs.

The cavity of the coelom is reduced by the presence of the alimentary canal, the digestive gland and the heart, but it is still spacious. It is partially divided up by certain mesenteries which support the alimentary canal, and it is traversed by several pairs of muscles. Some of these muscles run from valve to valve, and when they contract close the shell, others being situated behind the hinge, so that when they contract the valves slightly open. Others again run from the valves to the inner surface of the stalk and their contraction bends the body one way or another and may even serve to slightly rotate it. There are two large canals in the lophophore, one on each side which are also almost certainly coelomic in character, although in the adult they are shut off from the main coelom.

There is—except in one genus—but one pair of excretory organs. These are short tubes which open by large trumpet-shaped orifices (9, Fig. 175) into the coelom; while their external openings are situated at the sides of the body behind the lophophore. The cells lining the tubes are some of them ciliated, while others are crowded with coloured granules. As already mentioned, the genus *Rhynchonella* possesses two pairs of such organs.

As a rule, in Brachiopods the sexes are separated. The cells destined to form ova or spermatozoa are derived from those lining the body-cavity. At certain places, usually four in number, the coelomic cells multiply and build themselves up into ovaries or testes according to the sex. When they are ripe they fall off into the coelom and make their way to the exterior through the excretory organs which thus also serve as genital ducts. The spermatozoa are cast into the water by the male, and the female must bring them within the valves of her shell by the action of the current set up by the cilia, because the eggs are almost certainly fertilised as soon as they leave the excretory organs. The eggs develop in certain brood-pouches situated at the sides of the animal which are formed by a bulging in of the body-wall. A larva is ultimately formed which leaves the body of the mother and swims about in the sea by means of a band of cilia. As it is extremely minute, although it swims quickly it does not get very far, and this probably accounts for the fact that Brachiopods are usually found in large numbers in one place.

Distribution and Classification.

Brachiopods are found in all seas. About eleven genera have been dredged around the British Isles, most of them in comparatively shallow water. *Lingula* is usually found between tide-marks or in shallow water; it lives in a tube in the sand, and the bristles round the mouth of the shell doubtless serve to keep out particles of sand which might otherwise injure the animal. It is found along the East coast of America, in the Pacific and other places. One species of Brachiopod, *Terebratula wyvillei*, has been dredged from a depth of close upon 3000 fathoms.

Perhaps the chief interest of the group is that it includes an enormous number of fossil forms which had a very wide distribution. The extinct forms far surpass both in variety and number the existing forms. Some species have lived on,—as far as we can judge from the shell,—unchanged from the time when the earliest fossil-bearing rocks were laid down. They may thus claim to be one of the oldest groups with which we are acquainted.

The Brachiopoda are classified as follows:

Class I. Ecardines.

Shell with no hinge and no internal skeleton. The alimentary canal has an anus.

Ex. *Lingula*, *Crania*.

Class II. Testicardines.

Shell with hinge and internal prolongations, chiefly calcareous. No anus.

Ex. *Terebratula*, *Argiope*, *Waldheimia*, *Rhynchonella*.

CHAPTER XVI

PHYLUM POLYZOA

This group includes a great number of species, the individuals of which are so small as to be barely visible to the naked eye, but they are all colonial in their habits and the colonies usually attain a fair size. These colonies take many shapes, some branching like a tree, others being flattened like a leaf, while others again are discoidal; often they are encrusting, that is to say they form a layer on some seaweed or rock, for the majority of them are marine.

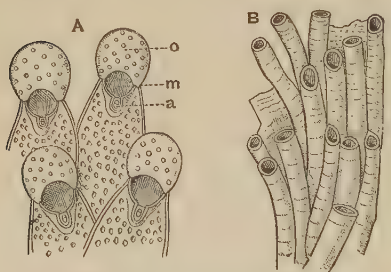

Fig. 177. Portions of two Polyzoan colonies. Magnified.

A. *Smittia landsborovii*. a. Avicularium. m. Orifice of cell. o. Ooecium or pouch in which the egg develops.
B. *Tubulipora plumosa*. After Hincks.

If one of these colonies be dried so that the organic matter shrivels up, a hard skeleton remains, and this is then seen to consist of a number of chambers or "cells," each of which opens to the exterior by an orifice, and, as a rule, communicates with its neighbours. The skeleton may be calcareous, or chitinous, or the colony may be gelatinous in consistency. The dried cell may be open or closed by a lid termed the operculum. During life each of these cells lodges part of the body of a person of the colony, the "cell" being indeed the cuticle; part however of the person is not clothed with cuticle and is normally stretched out above the cell—the opening in the dried cell is in fact the place where the flexible part of the person begins. At the end of this flexible part is the mouth surrounded by a ring of ciliated tentacles: on one side is the anus. The flexible part is termed

the polypide, and the cell the zooecium. If the polypide be retracted, which occurs when it is irritated, the anterior end is inverted and forms the tentacle sheath in which the tentacles lie. The operculum when present is a movable fold of the body-wall thrown back when the polypide is pushed out, and covering the opening of the tentacle sheath when it is retracted.

The animal within the cell has a U-shaped alimentary canal, the anus being situated not far from the mouth, but it is separated from it by a ring of tentacles in the centre of which the mouth lies. This crown of tentacles, called the lophophore, is not always circular, but may be drawn out into a horseshoe-shaped structure (Fig. 178), and in the subdivision of the group (Phylactolaemata) in which it undergoes this modification there is a small projection, called the epistome, which overhangs the mouth, being situated inside the tentacle ring. The tentacles are ciliated, and the action of the cilia brings food to the mouth, which leads into an oesophagus also ciliated, and this enlarges into a rounded stomach usually produced into a caecum (Fig. 178). From this a small intestine, parallel with the oesophagus, leads to the anus. From the aboral side of the stomach a cord of mesodermic tissue, called the funicle, usually passes to the body-wall.

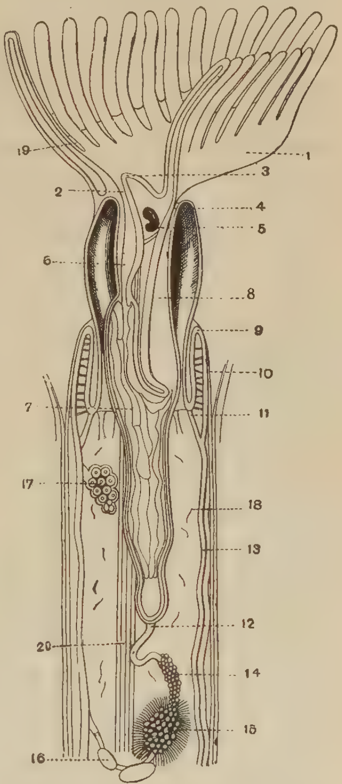

Fig. 178. View of right half of *Plumatella fungosa*, slightly diagrammatic. After Allman and Nitsche.

1. Lophophore. 2. Mouth. 3. Epistome. 4. Anus. 5. Nerve-ganglion. 6. Oesophagus. 7. Stomach. 8. Intestine. 9. Edge of fold of body-wall. 10. Wall of tube. 11. Muscles. 12. Funiculus. 13. Body-wall. 14. Testis. 15. Testis, more mature. 16. Statoblast. 17. Ovary. 18. Spermatozoa free in body-cavity. 19. Tentacles. 20. Retractor muscle.

The body-cavity is regarded as truly coelomic. It contains a fluid in which cells float; it is traversed by the funicle and often also by numerous strands of mesodermic tissue. The funicle may be the remains of a median mesentery which once separated the coelomic sacs of the two sides. Some of the cells of its walls give rise to reproductive cells, and the body-cavity opens to the exterior in certain individuals which possess an ovary by a short tubular duct, the so-called inter-tentacular organ. This functions as an oviduct and has been regarded by some authors as a modified excretory organ. A portion of the body-cavity is separated from the rest by a horizontal septum, and forms a space at the base of the tentacles into which the cavity of each tentacle opens. This may open into the other part of the coelom or may be completely shut off from it.

No heart or blood-vessels are present. It is possible that some of the nitrogenous waste matter may be got rid of by means of the inter-tentacular organ, but it has also been suggested that these waste products are stored up in certain cells on the funicle. From time to time the tentacles, alimentary canal and nervous system of an individual undergo degeneration and form a brown mass, called the brown-body, which forms a conspicuous feature in the colony. After a time the body-wall, which has not disintegrated, forms a new set of digestive organs and the brown-body may come to lie in the stomach of the reconstituted individual. Thence it passes to the exterior through the anus. It is thought that much of the waste matter which has accumulated in the body of the animal is, in this way, eliminated. In certain Phylactolaemata there is a pair of small coelomiducts which probably serve as excretory organs opening between the mouth and the anus.

A nerve-ganglion lies between the mouth and anus, situated in that part of the body-cavity which runs round the base of the lophophore.

Polyzoan colonies are usually hermaphrodite. The testes are as a rule formed by the multiplication of the coelomic cells which form part of the body-wall, while the ovary originates from the funicle or from the body-wall. They may be found in the same individual or in different individuals of the same colony. As a rule the eggs develop within some part of the parent colony, but they may be laid, escaping from the body-cavity through the inter-tentacular canal, and then they pass at once into the sea-water. More usually the early stages of development are passed through in the tentacle-sheath or in a special pouch called an ooecium (Fig. 177),

or in certain "cells" which contain rudimentary individuals. A free-swimming larval form is usually found, which after a time comes to rest and by budding forms a new colony.

Just as in the colonies of Hydrozoa we found different individuals set apart to perform different functions, so in Polyzoa we find a similar specialisation. Certain individuals may be modified to accommodate and protect the developing egg, but perhaps the most remarkable modifications are the vibracula and avicularia of the Cheilostome Polyzoa. The vibracula are long hair-like processes which sweep through the water; the avicularium consists of two snapping jaws provided with powerful muscles, like the claws of a lobster or the beak of a parrot (Fig. 179). They are modifications of a "cell" and its operculum. The avicularia occasionally catch worms, Crustacea and other animals whose presence might interfere with the colony, and by their action they probably prevent the larvae of encrusting animals settling on the Polyzoan colony. They thus serve somewhat the same purpose as the pedicellaria of Echinodermata, although they are widely different in structure.

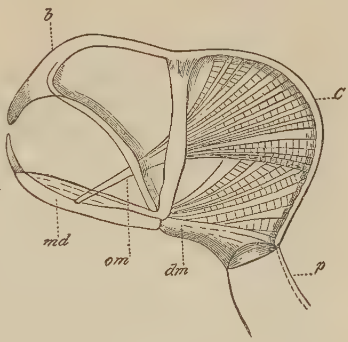

FIG. 179. An avicularium of *Bugula*. Magnified. From Hincks.

b. Beak. *c*. Chamber representing the body-cavity of the modified individual. *dm*. Muscle which opens, *om*. muscle which closes the mandible on the beak. *md*. Mandible, the operculum of the modified cell. *p*. Stalk.

Besides the sexual method of reproduction just mentioned certain internal buds termed statoblasts are formed in the group Phylactolaemata. Masses of cells arise from the funicle and become enclosed between two watchglass-shaped chitinous shells whose edges are kept together by a special ring of cells. As a rule, the Phylactolaemata die down during the winter, but the statoblasts persist and when spring recurs give rise to new colonies. A somewhat analogous process ensures the perpetuation of the species in certain fresh-water Ctenostomata.

Polyzoa are widely distributed throughout the sea, many occurring in shallow water, but others have been dredged at great depths. The Phylactolaemata and a few genera from other

subdivisions are fresh-water. Fossil forms are numerous and the Coralline Crag, a tertiary deposit, takes its name from the large number of coral-like calcareous forms, sometimes described as "corallines," which are found in it.

There is a small class of animals regarded by many zoologists as a division of Polyzoa, but which seems to others (with whom we are inclined to agree) to be a completely independent group of animals. These animals have no coelomic space, and both ends of the alimentary canal are included in the ring of tentacles; from this circumstance they derive the name (lit. anus inside) ENTOPROCTA. In this class the body consists of a stalk and a "cup." The edges of the latter are fringed with a short row of ciliated tentacles surrounding a disc on which both the mouth and the anus open. When irritated these tentacles are bent inwards and the contraction of a sphincter muscle causes the edge of the disc to be drawn over them exactly as happens in a Sea-anemone. Sometimes in *Pedicellina* the "cup" falls off and a new one is formed. Beneath the disc is situated a nerve-ganglion and the genital organs are continuous with a short duct which opens in the centre of the disc. The excretory system consists of a pair of true nephridia ending internally in flame-cells, which open between the mouth and the anus.

All other Polyzoa are grouped together as ECTOPROCTA, and these are subdivided into

Order I. **Gymnolaemata.**

With a few exceptions marine and having a circular lophophore. Devoid of an epistome.

Sub-order (1), **Cheilostomata.** An operculum covers the orifice of the cell. Avicularia and vibracula often present. Skeleton with more or less calcareous deposit in it.

Sub-order (2), **Cyclostomata.** Cells tubular and ending in circular mouths. No operculum. Calcareous skeleton.

Sub-order (3), **Ctenostomata.** Body-wall soft. The orifice of the cell is closed by the coming together of a membrane, which is often beset with a fringe of spines.

Order II. **Phylactolaemata.**

Fresh-water forms with a horseshoe-shaped lophophore (except *Fredericella*), an epistome, and statoblasts.

CHAPTER XVII

PHYLUM CHAETOGNATHA

The Chaetognatha (χαίτη, hair; γνάθος, jaw) are small cylindrical animals which swim at the surface of the sea. The name is suggested by the circumstance that at the sides of the mouth are two rows of curved movable bristles by means of which they seize their prey (*e*, Fig. 180).

The body has a small rounded head in front and tapers to a tail posteriorly; it is provided with one or two pairs of flat, lateral expansions termed fins; the general shape resembles that of a torpedo, if we leave the head out of account. It has also been compared to an arrow, and the popular term "Arrow-worm" has been applied to these animals. The head is surrounded by a fold of the skin forming a hood which is most prominent at the sides and dorsal surface. Within the hood the head bears on each side a row of sickle-like hooks whose points when at rest converge around the mouth, but are capable of being widely divaricated. The head also bears one or more rows of stout spines whose number and arrangement are of importance for the system of classification (*f*, Fig. 180).

The coelom is well developed and contains a fluid in which cells float. In strictness there are three pairs of coelomic sacs separated from one another by transverse and longitudinal partitions. In the head the coelomic space is practically obliterated by the great development from its walls of the muscles which move the hooks. The coelom of the trunk and tail is further divided into right and left halves by a vertical mesentery, which in the trunk region supports the alimentary canal (Fig. 181). This mesentery is pierced by numerous small holes.

The skin is covered by an epithelium more than one layer thick, some of the cells of which are modified to form sense-organs, while

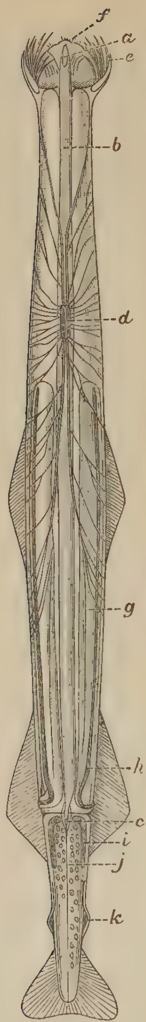

FIG. 180. A ventral view of *Sagitta hexaptera* × 3½. From O. Hertweg.

a. Mouth. *b.* Intestine. *c.* Anus. *d.* Ventral ganglion. *e.* Movable bristles on the head. *f.* Spines on the head. *g.* Ovary. *h.* Oviduct. *i.* Vas deferens. *j.* Testis. *k.* Vesicula seminalis.

others project from the surface of the body and are known as adhesive cells (Fig. 181). Beneath the epithelium is a thin layer of jelly called the basement membrane, and beneath this a layer of muscles. Anteriorly the muscles are broken up into numerous bundles which fill the cavity of the head, but in the trunk and tail the muscles form four distinct bundles, bilaterally arranged, two dorsal and two ventral.

There are no circular muscles either in the skin outside the coelom or surrounding the gut. Hence no peristalsis can take place, and this is the reason that the intestine is ciliated, for the action of the cilia is necessary to propel the food through it. Arrow-worms progress by alternate bendings of the body first to one side and then to the other very much as fish do, the stiff cuticle acting the same part in the Arrow-worm as the back-bone in a fish, i.e. of enabling the body to spring back into its original form, when the contraction of the muscle ceases.

The nervous system consists of a dorsally placed ganglion in the head which gives off two lateral nerves; these pass round the alimentary canal and end in a ventral ganglion situated (Figs. 180 and 181) near the centre of the body. The cerebral ganglion gives off nerves to the eyes, the olfactory organ, muscles, etc., and both it and the ventral ganglion are connected with a tangle of nerve-fibrils lying at the base of the ectoderm. A pair of eyes exist on the upper part of the head, and behind the eyes an organ to which an olfactory function has been assigned. This consists of a ring

of modified ciliated epithelium. Clumps of isolated tactile cells with long hairs surrounded by supporting cells are scattered over the body and fins (Fig. 181).

The alimentary canal is simple and straight. The mouth—with one exception—is ventral and it leads into a pharynx which traverses the head; this passes into an intestine lined by a single layer of ciliated epithelium amongst which are some glandular cells. The anus is situated at the junction of the trunk and the tail and is ventral.

In *Spadella marioni* there is a glandular structure in the head which may be connected with the excretion of waste nitrogenous

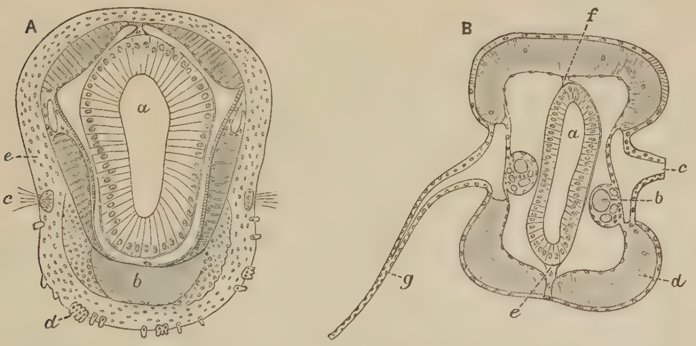

FIG. 181. A. Transverse section through a *Spadella cephaloptera* in the region of the ventral ganglion × about 200. B. Transverse section through a *Sagitta bipunctata* in the region of the ovary × about 120.

a. Intestine. *b.* in A. Ventral ganglion. *b.* in B. Ovary. *c.* in A. A ciliated sense-organ. *c.* in B. Base of the left fin which has been cut off. *d.* in A. Adhesive cells. *d.* in B. Left ventral muscle. *e.* in A. Ectoderm. *e.* in B. Ventral mesentery. *f.* Dorsal mesentery. *g.* Right fin.

material, but no other excretory organ is known and no special respiratory or circulatory organs exist.

The Chaetognatha are hermaphrodite. The paired ovaries (Figs. 180 and 181) lie in the trunk region of the body-cavity supported by a lateral mesentery. When mature they almost fill the cavity. The oviduct traverses the ovary. When the ova are ripe they burst their way into the oviduct, and are fertilised in it, for spermatozoa have been found in the oviduct. The oviducts open to the exterior at the upper surface of the lateral fin, just where the trunk passes into the tail.

The median mesentery of the trunk region is continued through the tail, dividing its cavity into two; and in each of these lateral

cavities the cells lining the body-wall are heaped up and form a testis (*j*, Fig. 180). The cells divide up into spermatozoa, which float in the coelomic fluid and are kept in motion by some of the ciliated cells lining the body-cavity. The spermatozoa escape through a pair of short vasa deferentia which open on the one hand into the coelom and on the other to the exterior on the tail. Each has on its course a well-marked vesicula seminalis (Fig. 180).

The ova are transparent and pelagic. The cells destined to form the reproductive organs of the adult are early set apart and distinguishable. The development is entirely embryonic, no larval form being recognisable.

The Chaetognatha consist of three genera, *Sagitta*, *Spadella* and *Krohnia*, amongst which some twenty-three species are divided. The genera differ from one another chiefly in the arrangement of the armature on the head and in the disposition of the fins, which are always horizontally placed and supported by fine skeletal rods. A caudal fin exists in addition to one (*Spadella* and *Krohnia*) or two (*Sagitta*) pairs of lateral fins.

The Chaetognatha are with hardly an exception pelagic, that is they live near the surface of the sea, and as is usually the case with animals which frequent the surface of the ocean they are transparent. At certain times of the year they are found in incredible numbers swimming on the surface by the muscular contraction of their bodies, their fins acting as balancers and having no movement of their own. At other seasons they descend and are taken at depths varying from 100 to over 1000 fathoms. The cause of their descent is unknown. Their food consists of Infusoria, small larvae and small Crustacea.

The zoological position of the Chaetognatha is obscure. They show no relationship with any of the larger groups; possibly their nearest existing allies are to be found amongst certain aberrant Nematoda, such as *Chaetosoma*, but at present too little is known to make any close comparison possible.

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CHAPTER XVIII

INTRODUCTION TO THE PHYLUM VERTEBRATA, SUB-PHYLA HEMICHORDA, CEPHALOCHORDA AND UROCHORDA

Characters of the Phylum.

The Vertebrata comprise almost all the larger animals, including Man. The name simply means jointed (Lat. *vertebra*, a joint, and especially a bone of the spinal column), and refers to the possession of a jointed internal axis as the main part of the skeleton. In the lowest forms this axis is not developed, but in place thereof there is a smooth elastic rod, which has received the name of notochord, literally back-string (Gr. νῶτον, back; χορδή, string). In all the members of the phylum this notochord is present at some stage of development, although in the higher forms it subsequently becomes surrounded and obliterated by the jointed rod or vertebral column. Hence the name Chordata, which has been proposed for the group, is really more appropriate; but as the term Vertebrata has been sanctioned by long usage it is inadvisable to depart from it.

Besides the possession of the notochord there are two other features by which the Vertebrata are distinguished. One of these is that all Vertebrata possess at some period of their lives slits in the wall of the front part of the alimentary canal. In the lower and more simply organised members of the phylum these slits allow the water which is taken in at the mouth for purposes of respiration to escape, and hence they are called gill-slits. The other feature common to all Vertebrata is that the main mass of the nervous system takes on the form of a dorsal strip of sensitive skin—the medullary plate, which becomes wholly or partly enrolled to form a tube, the neural canal or spinal cord.

There are in all about 32,000 known species of Vertebrata, including all the more familiar animals—fish, frogs, reptiles, birds and mammals; so that the word animal to the ordinary mind

generally calls up the idea of a vertebrate. Nevertheless the number of species is not much more than half that of the Mollusca and is not a tenth that of the described species of Arthropoda.

Sub-phylum I. HEMICHORDA.

The most primitive members of the phylum are certain worm-like forms and certain sessile animals, in which it has taken special research to discover traces of Vertebrate structure. The sessile forms obtain their food like the Polyzoa by means of currents produced by cilia clothing arborescent outgrowths of the body. The worm-like forms live in mud, passing it through their intestines and extracting nutriment from the organic matter it contains: thus they feed and move forwards by the same process. Both groups are marine. These animals are termed Hemichorda (Gr. ἥμι, half) on account of the short rudimentary notochord which they possess. Sometimes they are called Enteropneusta (Gr. πνεῦμα, breath) because, like all Vertebrata, they use the anterior portion of the gut for breathing. There are two orders: the Balanoglossida, which are worm-like and burrow in mud, and the Cephalodiscida, which are sessile and live in clear water and construct tubes for themselves in which they live, and superficially resemble Polyzoa. The Balanoglossida are divided into several genera, *Dolichoglossus*, *Chlamydothorax*, *Glossobalanus* and others; these genera have resulted from the splitting up of the old genus *Balanoglossus*, which is sometimes still used as a semi-popular designation for any member of the order. We shall describe a Balanoglossid as a type of the Hemichorda.

The body of the animal is divided into three portions: (1) a conical anterior part in front of the mouth, termed the proboscis; (2) a swollen cylindrical portion immediately behind the mouth, termed the collar; and (3) a long trunk, at the end of which is the anus (Fig. 182).

The proboscis contains one, and the collar and trunk each a pair of special sections of the coelom or body cavity. The coelomic sacs of the proboscis and collar communicate with the exterior by ciliated tubes, termed the proboscis and collar pores respectively (Figs. 183 and 184). The cilia lining these tubes produce currents setting inwards: thus the collar and proboscis are kept swollen up and tense with water and form efficient burrowing instruments. If one of the Balanoglossida be removed from the

water and laid upon damp sand it is incapable of burrowing and wriggles helplessly about. As soon however as it is covered by water the proboscis and collar are seen to dilate and become stiff, and the proboscis is then inserted into the sand, soon followed by the collar, whilst the trunk is dragged passively after them. As

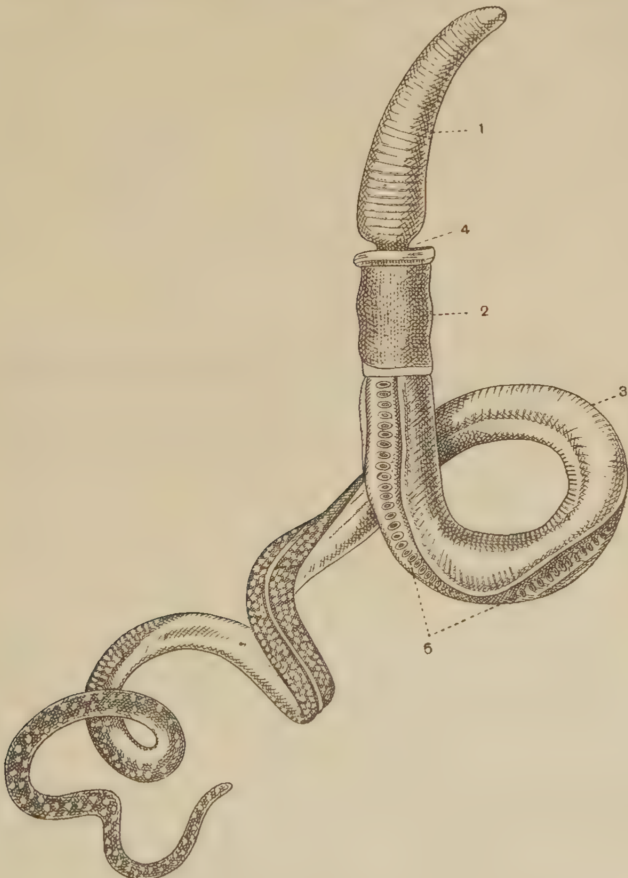


FIG. 182. A *Dolichoglossus kowalevskii* × 1. From Spengel.
1. Proboscis. 2. Collar. 3. Trunk. 4. Mouth. 5. Gill-slits.

the walls of both proboscis and collar are highly muscular the water can be expelled through the pores and the volume of these regions of the body diminished, but the action of the cilia soon swells them up again. On the hinder wall of the proboscis cavity there is a puckered membrane richly supplied with blood-vessels,

which is called the glomerulus and appears to act as a kidney. When the water in the cavity has become impregnated with excretory products it is expelled as explained above by a muscular contraction.

The alimentary canal runs straight from the mouth on the anterior surface of the collar region to the posterior end of the trunk; there is neither stomodaeum nor proctodaeum. In most species in the anterior part of the trunk the canal has an 8-shape in section, being partially constricted into two tubes, an upper or branchial into which the gill-slits open, and a lower or oesophageal along which the mud is passed which the animal has swallowed for food. The notochord is a hollow tube of cells surrounded by a tough membrane much thickened beneath (Fig. 183). This tube opens

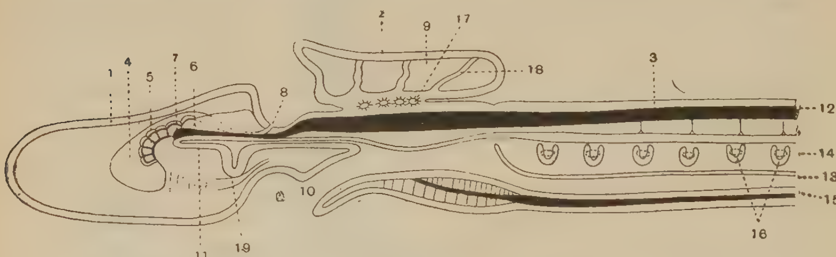


FIG. 183. Longitudinal vertical section through the middle line of *Glossobalanus*. Diagrammatic.

1. Proboscis. 2. Collar. 3. Trunk. 4. Proboscis cavity. 5. Glomerulus. 6. Pericardium. 7. Heart. 8. Proboscis pore. 9. Collar cavity. 10. Mouth. 11. Notochord. 12. Dorsal blood-vessel. 13. Oesophageal portion of alimentary canal. 14. Branchial region of alimentary canal. 15. Ventral blood-vessel. 16. Gill-slits showing external and internal openings; the outlines of the external openings are dotted. 17. Central nervous system. 18. Dorsal roots of nervous system. 19. Ventral pocket of proboscis cavity.

behind into the alimentary canal in the collar region and projects forward into the proboscis as a support for this organ, which is attached by a very narrow neck to the collar. The whole skin is sensitive, since there is everywhere a layer of nerve-fibrils underlying the ectoderm cells, but this fibrillar layer is especially thickened along the mid-dorsal and mid-ventral lines of the trunk, these two regions being connected by a ring of nervous tissue immediately behind the collar. The dorsal thickening alone is continued into the collar region, and here it becomes rolled up so as to constitute a short neural tube (Fig. 183) which becomes detached from the ectoderm and assumes a deeper position; it may retain however a

connection with the ectoderm through several strings of cells with a fibrillar sheath, known as dorsal roots (18, Fig. 183).

There are very numerous gill-slits opening into the alimentary canal, in the front part of the trunk region; they ought rather to be called pouches with a small outer and a large inner opening. The inner opening of each pouch is divided almost into two by a tongue projecting down from its dorsal edge, the so-called tongue-bar. This tongue-bar is specially richly supplied with blood-vessels, especially on its outer surface, and so may be regarded as the principal respiratory organ. It may be doubted indeed if the principal function of the gill-clefts in the Balanoglossida be really respiratory. These openings seem rather to be intended to filter off the water from the wet mud which is swallowed as food. The blood-vessels are destitute in most cases of any proper wall: they are as it were mere crevices between the epithelial walls of the gut, coelom and skin. There is however a well-defined contractile dorsal channel running forward into the kidney, the contractility being confined to the front end in the proboscis, where there is a closed sac with muscular walls, which pulsate rhythmically, situated above the blood-vessel. The sac is termed the pericardium, and the dilated part of the blood-vessel below it, the heart. This dorsal vessel communicates with a ventral vessel in the trunk region by two descending curved vessels at the sides of the collar. Each of the coelomic cavities of the trunk sends forwards into the collar region a narrow tongue lying at the side of the blood-vessel. These tubes from their relation to the vessel are called perihaemal tubes (Gr. περί, around; αἷμα, blood).

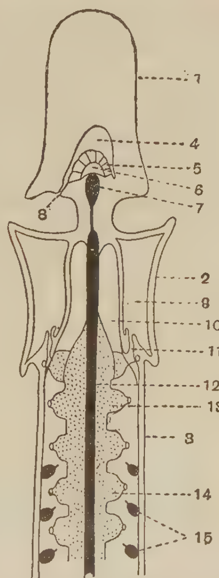


FIG. 184. Longitudinal horizontal section through *Glossobalanus*. Diagrammatic.

1. Proboscis. 2. Collar. 3. Trunk. 4. Proboscis cavity. 5. Glomerulus. 6. Pericardium. 7. Heart. 8. Proboscis pore. 9. Collar cavity. 10. Perihaemal cavity. 11. Collar pore. 12. Dorsal blood-vessel. 13. Alimentary canal. 14. Branchial sac with external opening. 15. Reproductive organs.

The genital organs or gonads are mere packets of cells in the gill region and behind it, developed from the wall of the trunk coelom (Fig. 184). Each when ripe forms its own opening through the body-wall.

The Cephalodiscida exhibit the same three regions of the body as the Balanoglossida, but these are very differently developed. The proboscis becomes a flat glandular shield bent down over the mouth. It secretes the material out of which the house or tube is constructed. The collar region is prolonged into hollow arms which are beset by rows of ciliated tentacles which waft microscopic swimming organisms into the mouth. The central nervous system remains as a plate of exposed ectoderm. The trunk is short and rounded and the anus is shifted on to the dorsal surface. There is never more than a single pair of gill-pores, and in minute forms these may be absent. From the ventral surface springs a stalk from which buds are produced which grow up into new persons.

Prof. Gilchrist has shown that the individuals of a Cephalodiscid colony can emerge from their tubes and creep out. They fix themselves to the substratum by the ventral surface of their praeoral lobes or proboscides exactly as the larva of an Asteroid does. (See p. 366.)

Cephalodiscus with twelve arms and one pair of gill-pores is fairly abundant in the Antarctic and Southern Atlantic Oceans.

Rhabdopleura, with two arms and no gill-pores, which is found fairly abundantly in moderately deep water in the North Sea, was formerly described as a Polyzoon. The absence of gill-pores in *Rhabdopleura* is no doubt a secondary modification due to the very small size of the individuals, for we find that as the size of animals of the same build is diminished, respiratory organs tend to disappear.

One point of interest attaching to the Hemichorda is that they may commence life as free-swimming larvae, resembling the larvae of the Echinodermata, and suggesting the thought that perhaps two such different groups as the Vertebrata and Echinodermata may have descended by different paths from the same simple free-swimming ancestors.

In dealing with the larvae of Echinodermata it was pointed out that the middle section of the coelom called the hydrocoele, which develops into the water-vascular system of the adult, has been compared to the collar coelom of Hemichorda. This comparison is supported by the condition of the collar region in Cephalodiscida, where, as we have seen, it is produced into outgrowths very like the radial canals of Echinodermata and beset with tentacles which may be compared to tube feet.

Sub-phylum II. CEPHALOCHORDA.

Leaving the Hemichorda we next come to some small fish-like animals, the Cephalochorda, which were formerly all included under the name *Amphioxus*, and indeed there is no very strong reason for breaking up this old genus. The name *Amphioxus*

at both ends; ὀξύς, sharp) refers to the shape of the body, which is long, flattened and pointed at both ends (Fig. 185). It is remark-

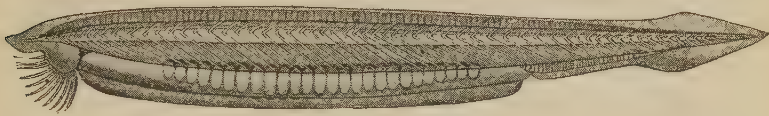
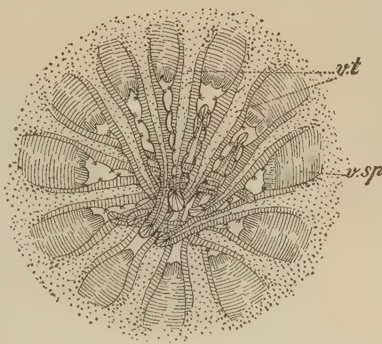
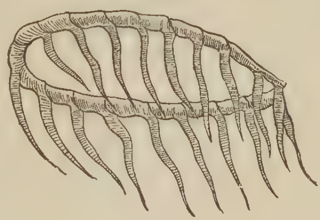


Fig. 185. *Amphioxus lanceolatus* from the left side, about twice natural size. After Lankester. The gonadic pouches are seen by transparency through the body-wall; the atrium is expanded so that its floor projects below the metapleural fold; the fin-rays of the ventral fin are indicated between the atrial pore and anus. The dark spot at the base of the fifty-second myotome represents the anus.

able that we here meet for the first time with a shape very common among Vertebrates, but very uncommon elsewhere in the animal kingdom, viz. a laterally compressed form with narrow ventral and dorsal regions and deep sides. It is common to find animals with broad backs and bellies and narrow sides, but rare except amongst Vertebrates to find the reverse condition. In consequence of this peculiar shape *Amphioxus* falls on its side when it ceases moving. It burrows in the sand, lying with its mouth just protruding, and as its lips are fringed with ciliated rods (Fig. 186) a current is produced which brings new water to the gills and with it small swimming organisms which serve as food. At night *Amphioxus* often leaves its burrow and swims about, returning instantly to the sand if alarmed. It can burrow with either the head or tail.



A



B

Fig. 186.

A. Velum of *Amphioxus* seen from the inside of the pharynx. After Lankester.
v.sp. sphincter muscle of velum.
v.t. velar tentacles lying across the oral opening.

B. Oral cartilages of *Amphioxus*. After J. Müller. The basal pieces lie end to end in the margin of the oral hood, and each basal piece sends up an axial process into the corresponding oral cirrus.

The notochord is a smooth cylindrical rod lying above the gut and running from end to end of the animal. It consists of cells, the greater part of the bodies of which are changed into a gelatinous substance, and which are surrounded by an exceedingly firm membrane termed the chordal sheath. In the embryo the notochord first appears as a groove in the dorsal wall of the gut, so that we may say that the notochord of the Hemichorda retains a form which is passed through in development by that of *Amphioxus*.

In the very young embryo also an indication is seen of the division of the body into the same three regions as we found in the Hemichorda. Just as in the embryo of Balanoglossida so here, the embryonic gut gives rise to five outgrowths from which the coelom of

Posterior

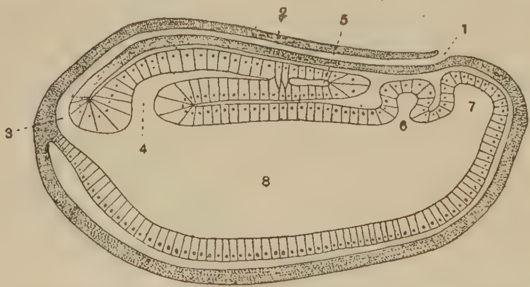


Fig. 187. Diagrammatic longitudinal section of an embryo of *Amphioxus*.

1. Neuropore—anterior opening of the neural canal. 2. Neural canal. 3. Neurenteric canal. 4. Coelomic groove. 5. Somite divided off from coelomic groove. 6. Collar cavity. 7. Head cavity. 8. Alimentary canal.

the adult is derived. These outgrowths are (1) a median anterior bilobed pouch, corresponding to the proboscis cavity of Balanoglossida; this divides at once into two, giving rise to the so-called head cavities; (2) an anterior pair of pouches, the collar cavities, corresponding to the similarly named sections of the coelom of Balanoglossida; and finally (3) a pair of groove-like extensions of the dorso-lateral angles of the gut cavity, called the coelomic grooves, developed only at the hinder end of the gut. From the last-named the coelom of most of the body arises, and they correspond to the trunk coelom of Balanoglossida (Fig. 187). The proboscis or prae-oral region is however very small and bent down ventrally; its cavity becomes more or less obliterated in the adult. Dorsally the collar region is narrow from before backwards, but it extends obliquely downwards and backwards, and here becomes fused with the lower divisions of the trunk cavities. (*v. infra.*)

The upper and anterior portion of the collar cavity becomes separated from the rest : its inner walls thicken and develop into a powerful longitudinal muscle which forms the first myotome (Gr. *μῦς*, muscle ; *τόμος*, a division).

The trunk coelomic cavity breaks up from the beginning into a series of pouches called somites, each of which subsequently divides into an upper and an under part. The inner walls of the upper parts undergo a similar change to that experienced by the corresponding part of the collar cavity, forming a series of myotomes. The name myotome is given to each of the metamerically arranged bundles of muscle-fibres. Each myotome is separated from the next by a connective-tissue partition. In *Amphioxus* the myotomes of the right side alternate with those of the left, so that the centre of a myotome on one side is opposite the connective-tissue partition on the other. Each is V-shaped, and they are arranged so <<<.

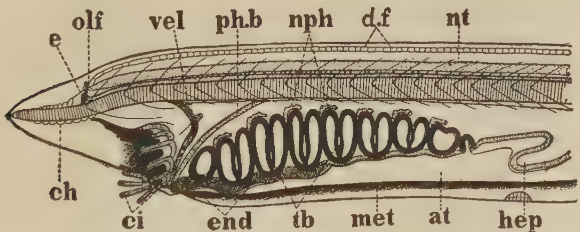


FIG. 188. Anterior region of young *Amphioxus* from left side. After Willey ; the renal tubules inserted after Boveri.

at. Atrial cavity. *ci.* Oral cirri. *ch.* Notochord. *d.f.* Dorsal fin-chambers. *e.* Eye-spot. *end.* Endostyle. *hep.* Outgrowing liver ; the index line passes through one of J. Müller's "renal papillae." *met.* Metapleural fold. *nph.* Nephridia. *nt.* Spinal cord. *olf.* Olfactory pit. *ph.b.* Peripharyngeal ciliated band. *tb.* Tongue-bars. *vel.* Velum.

Hence in a transverse section several myotomes are seen on each side of the body. Thus we have two great series of longitudinal muscles broken up into myotomes, one on each side of the animal, by the alternate contraction of which powerful side-strokes of the flat body propel the animal forwards. The elasticity of the notochord acts like a fly-wheel in storing the force during the latter part of each stroke and reinforcing each stroke at its commencement. The cavity of the upper division of the somite persists throughout life, and is known as the myocoel and the fold separating it from

the cavity of the lower division is termed the intercoelic membrane (*i.m.* Figs. 190 and 196).

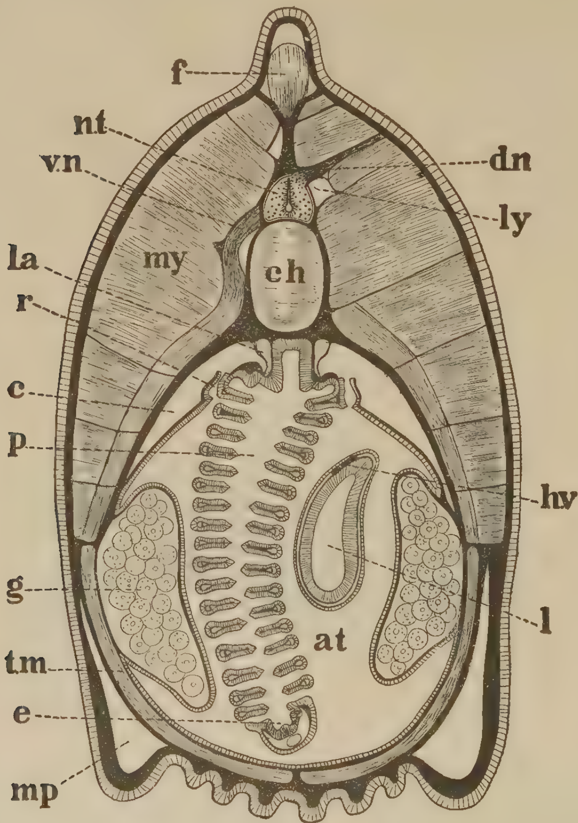


FIG. 189. Diagrammatic transverse section through pharyngeal region of a female *Amphioxus*. After Lankester and Boveri, from R. Hertwig.

at. Atrial cavity. *c.* Dorsal coelom, separated from atrial cavity by the double-layered membrane known as the *ligamentum denticulatum*. *ch.* Notochord. *d.n.* Sensory nerve. *e.* Endostyle, below which is the endostylar coelom containing the ventral aorta. *f.* Fin-ray of dorsal fin. *g.* Gonadic pouch containing ova. *h.v.* Hepatic vein lying in the narrow coelomic space which surrounds *l*, the liver or hepatic coecum. *l.a.* Left aorta separated from the right aorta by the hyperpharyngeal (epibranchial) groove. *ly.* Lymph-space. *mp.* Metapleural fold, containing a lymph-space. *my.* Longitudinal muscles of myotomes; over against the dorsal coelom these muscles are arranged vertically, and form the rectus abdominis of Schneider. *n.t.* Spinal cord. *p.* Pharynx. *r.* Nephridium. *t.m.* Transverse or subatrial muscles. *v.n.* Motor spinal nerve, the fibres of which have the appearance of passing directly into the muscle-fibres. N.B. The connective tissue (cutis, notochordal sheath, etc.) and the coelomic epithelium are indicated by the black lines.

The lower portions of the somites fuse with one another and form a continuous body cavity round the hinder part of the alimentary canal which is called the splanchnocoel (σπλάγχνον, entrail) (*b.c.* Fig. 190) with the anterior end of which the lower portions of the collar cavities fuse. In front, owing to the presence of gill-slits, there are formed a right and a left dorsal coelomic canal, and a ventral coelomic tube, or endostylar coelom, the dorsal and ventral portions communicating with one another by spaces in the gill-bars, that is, in the pieces of body-wall intervening between the gill-slits. These spaces are termed branchial coelomic canals (Fig. 198).

A ridge grows out on each side of the body into a flap, which meets its fellow beneath the ventral wall of the body and thus they enclose a space, the so-called atrial cavity (Figs. 189, 190). This still communicates with the exterior through the atrial pore. The gill-slits, which occur in the front part of the trunk region, open into this atrial cavity. The atrial flaps, enclosing the atrial cavity, are an obvious arrangement by which the slits are saved from being choked with the sand in which the creature lives. As in the case of Hemichorda, the slits of *Amphioxus* are divided into two, by a tongue-bar reaching from the upper margin almost to the bottom of the slit. Each slit thus becomes U-shaped (Figs. 188, 191).

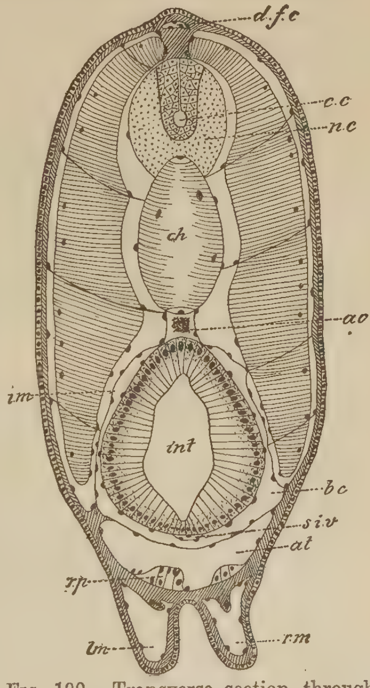


FIG. 190. Transverse section through post-pharyngeal region of young *Amphioxus*, to show groups of renal cells in floor of atrium. After Lankester and Willey.

ao. Aorta. *at.* Atrial cavity. *b.c.* Body-cavity (coelom). *c.c.* Central canal of nerve-cord (*n.c.*). *ch.* Notochord. *d.f.c.* Fin-cavity. *i.m.* Intercoelic membrane. *int.* Intestine. *l.m.* and *r.m.* Left and right metapleural folds. *r.p.* One of J. Müller's "renal papillae." *s.i.v.* Subintestinal vein.

The atrial flaps are at first formed entirely from the splanchno-

coelic region but they become invaded by the lower ends of the trunk myotomes; the ventral muscle however which runs across the under surface of the atrial cavity (Fig. 188), and which by contracting diminishes the size of this cavity and thus expels water, originates from the walls of the splanchnocoel.

The mouth is originally some distance behind the anterior end, and on the left side, so that there is a prae-oral portion of the body which in the embryo is occupied by an anterior division of the

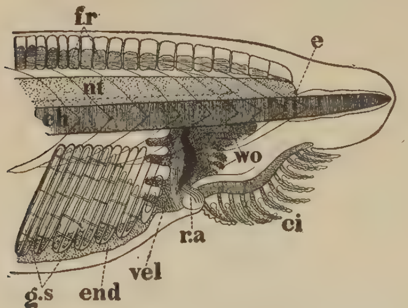


FIG. 191. Anterior portion of body of young transparent *Amphioxus*. After J. Müller, slightly altered.

ch. Notochord. *ci.* Oral cirri. *e.* Eye-spot. *end.* Endostyle. *f.r.* Fin-rays. *g.s.* Gill-slits; the skeletal rods of the gill-bars are indicated by black lines. *nt.* Spinal cord, with pigment granules near its base. *r.a.* Down-growth from right aorta lying to the right of *vel.* the velum, with velar tentacles projecting back into pharynx. *w.o.* Ciliated epithelial tracts on inner surface of oral hood.

FIG. 192. Anterior portion of spinal cord of *Amphioxus*; seen from above. After Schneider.

Between the first pair of cranial nerves is seen the eye-spot; one of the branches of the second pair of cranial nerves sometimes arises directly from the spinal cord as shown on the right; farther back are seen the pigment spots of the nerve-cord.

coelom corresponding to the proboscis cavity of the Hemichorda. Subsequently however the atrial flaps extend right to the anterior end, so that a new terminal mouth is formed leading into a chamber which is clothed by ectoderm and which is therefore to be regarded as the stomodaeum. The opening of the stomodaeum now forms the apparent mouth, and the lips of this secondary mouth grow out into rods supported by gelatinous material and covered with cilia, the so-called oral cirri, the function

of which has been already explained (Fig. 186). The walls of the stomodaeum are known collectively as the oral hood. The position of the primary mouth is still marked by a projecting lip, the velum, which is produced into ten or twelve delicate tentacles. These form a filter to prevent coarse material from reaching the alimentary canal.

The nervous system is a simple tube with thick walls and very narrow cavity. It is almost as extended as the notochord, and lies above it. It does not however quite reach the front end of the body. Its extreme front tip is called the cerebral vesicle; it has a wide cavity with thin walls, so that the total diameter is not

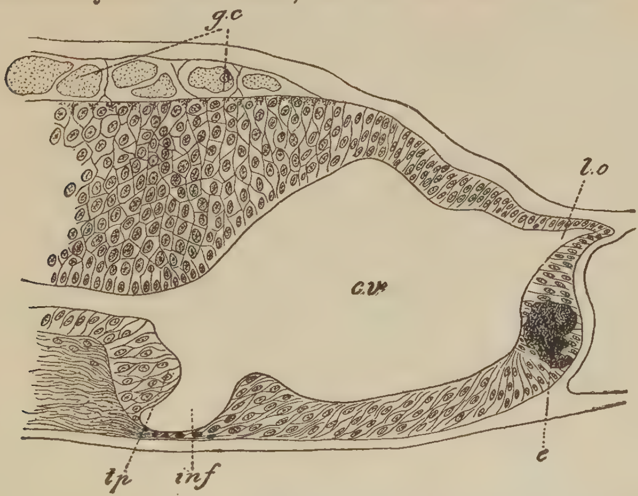


FIG. 193. Median vertical section through the cerebral vesicle of *Amphioxus*. After Kupffer.

c.v. Cavity of cerebral vesicle. *e.* Eye-spot. *g.c.* Dorsal group of ganglion-cells. *inf.* Infundibulum. *l.o.* Olfactory lobe. *tp.* Tuberculum posterius.

increased. There is a pit reaching down to it from the external skin, possibly a rudimentary olfactory organ (Fig. 193), and in the wall of the vesicle itself is a mass of pigmented cells forming an eye-spot. In the young larval *Amphioxus* this part of the nerve-tube remains for a considerable time as an uncovered medullary plate, and one is inclined to imagine that it corresponds to the sensitive nervous surface of the proboscis in the Hemichorda, since in the larvae of these animals there is a sensitive plate with two eye-spots at the apex of the prae-oral lobe. It must be remarked however that pigment cells in each of which a nerve-cell

is embedded are scattered at intervals all along the nerve-tube. It has been proved that *Amphioxus* is sensitive to light, but that it is equally sensitive if the front end containing the cerebral vesicle with its eye-spot be cut off. Therefore it is held, and in our opinion rightly, that all the pigmented spots in the nerve-cord are seats of light-sensation. In the wall of the nerve-tube are to be found two kinds of nerve-cells, viz., (*a*) ordinary small nerve-cells, the processes of which soon pass outwards into the peripheral

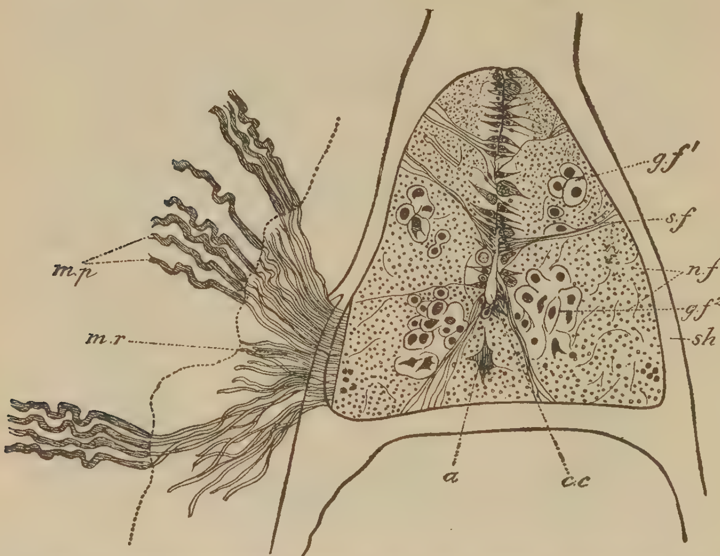


FIG. 194. Transverse section through the spinal cord of *Amphioxus* in the middle region of the body. After Rohde.

a. Giant fibre. *c.c.* Central canal. *g.f*¹, Giant nerve-fibres, which traverse the spinal cord from before backwards. *g.f*². Giant nerve-fibres, which traverse the spinal cord from behind forwards. *m.p.* Muscle-plates, i.e. terminations of the nerve-fibres on the muscles. *m.r.* Motor nerve-fibres. *n.f.* Longitudinal nerve-fibres cut across. *s.f.* Supporting cells. *sh.* Sheath of nerve-cord.

nerves, and (*b*) very large nerve-cells, the processes of which extend almost throughout the entire length of the nerve-tube. The processes of the latter kind of cell are called "giant fibres" ($g.f^1$ and $g.f^2$, Fig. 194): they appear to have to do with coordinating the muscular movements of the animal. Besides the nerve-cells, as in all nervous systems, there are a certain number of supporting cells (*s.f*, Fig. 194). In the embryo of *Amphioxus* the whole wall of the nerve-tube consists of a single layer of cells, all of

which abut on the cavity of the tube; many of these cells become afterwards transformed into small round nerve-cells, and recede from the cavity, assuming a more peripheral position: but others retain their connection with the cavity and become drawn out into fibre-like supporting cells. From the nerve-cord are given off two kinds of nerves, but not at the same level, so that in a transverse section one kind only is seen. These are: (1) sensory nerves, going directly to the skin and having a dorsal origin; (2) motor nerves, going to the myotomes. The nervous tube and the alimentary canal at first both reach to the extreme posterior end of the body and here are connected by a vertical tube, the neurenteric canal. On the course of this tube the anus is formed. As development proceeds the anus slowly shifts forwards and the neurenteric canal becomes a solid string of cells and disappears. Thus is initiated the formation of a tail, by which term is denoted a portion of the body devoted entirely to locomotion and freed from all part of the gut, being filled only with muscles. The tail of *Amphioxus* acquires only a very limited development, but it soon becomes surrounded by a tail fin, at first merely made up of the enlarged skin cells, but soon becoming a flap containing gelatinous material. A similar fold along the middle line of the back forms the dorsal fin, in which, in the larva, there are a series of metamerically arranged cavities lined by distinct epithelium, and although more numerous than the myotomes they are probably derivatives of

FIG. 195. *Amphioxus*. Nephridium of the left side, with the neighbouring portion of the pharyngeal wall, as seen in the living condition. The round bodies in the wall of the tubule represent carmine granules. Highly magnified. After Boveri.

the myocoelic cavities (*d.f.c.* Fig. 190).[1] There are also low fin folds projecting from the sides of the atrial cavity and constituting the lateral or metapleural fins (Fig. 189), and a median ventral fold between the atrial pore and anus, called the ventral fin (Fig. 185). The dorsal and ventral fins are stiffened by a number of gelatinous rods, and those in the dorsal fin are developed from thickenings of the cavities described above.

The alimentary canal of *Amphioxus* is a perfectly straight tube consisting of stomodaeum or mouth gut, pharynx or branchial gut, and intestine or digestive gut. The pharynx

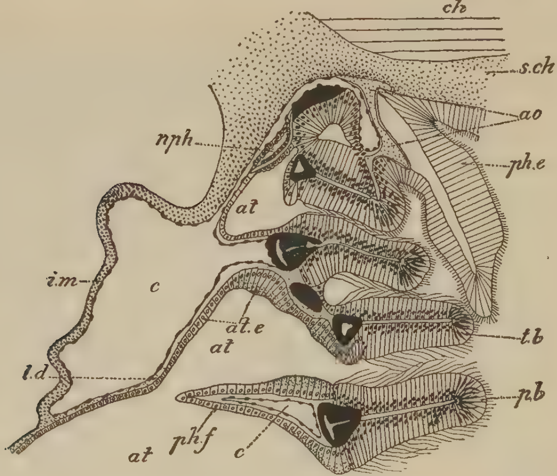


FIG. 196. Portion of transverse section through the pharynx of *Amphioxus*, to show position of excretory tubule. After Weiss.

ao. Left aorta. *at.* Atrial cavity. *at.e.* Atrial epithelium. *c.* Coelom. *ch.* Notochord. *i.m.* Intercoelic membrane. *l.d.* Dorsal wall of atrial cavity. *nph.* Nephridium. *p.b.* Gill-bar. *ph.e.* Epithelium of hyperpharyngeal groove. *ph.f.* Fold attached to gill-bar containing branchial coelomic canal. *s.ch.* Sheath of notochord. *t.b.* Tongue-bar.

has along both dorsal and ventral middle lines grooves lined with cilia connected with each other by a circular groove just inside the velum or true mouth. The ventral groove is called the endostyle or hypopharyngeal groove, the upper groove is termed the hyperpharyngeal, and the connecting groove the peripharyngeal band (Figs. 188, 189, 191). The function of these grooves is curious. The endostyle produces a cord of mucus which is worked forwards by its cilia and pressed up the sides of

[1] This supposition has recently been proved to be correct at least in the case of one species.

the peripharyngeal bands and the inner sides of the gill-bars. Here it is caught by the inrushing current of water produced by the cilia of the oral cirri and swept back along the hyperpharyngeal groove to the opening of the intestine, entangling in its passage the small plants and animals carried by the water; the latter of course escapes into the atrial cavity through the hundred or so long narrow gill-slits. The intestine is prolonged forward on the right side of the pharynx into a blind pouch, the so-called liver (*l*, Fig. 197), which probably secretes a digestive juice.

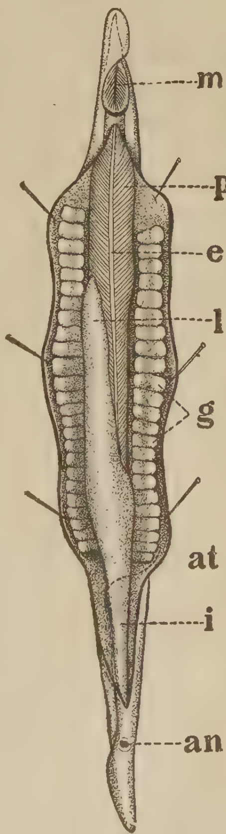


Fig. 197. *Amphioxus* dissected from the ventral side × 2. After Rathke, slightly altered.

an. Anus. *at*. Position of atrial pore; the extension of the atrium behind this point is indicated by the dotted line passing over to the right side of *i*, the intestine. *e*. Endostyle. *g*. Gonadic pouches. *l*. Liver. *m*. Entrance to mouth with the oral cirri lying over it. *p*. Pharynx.

The excretory organs of *Amphioxus* are small and have only recently been discovered. We have seen that in the region of the pharynx the coelom has become reduced to a narrow canal, beneath the pharynx, and to two dorsal canals at the sides of the notochord (Figs. 189, 190). At the level of each tongue-bar there projects into each of these canals a true nephridium of the type described in Platyhelminthes and Annelida. Each nephridium opens into the atrial cavity below by a short wide tube. Internally it divides into several branches which end blindly, each branch terminating in a tuft of those peculiar stalked flame cells known as solenocytes (Figs. 195, 198). One peculiarly large nephridium known as "Hatschek nephridium" lies in front of the velum above the buccal cavity but below the notochord. This nephridium opens into the pharynx. Besides these a number of thickened patches of the atrial epithelium, discovered by Johannes Müller and called by him renal papillae, are thought to assist in excretion (Figs. 188 and 190).

The blood system is exceedingly simple. The blood from the alimentary canal is brought back by a sub-intestinal vein, which like a broad river is often subdivided into two or three parallel channels which then reunite with one another; in a word it is more a plexus than a tube. It runs to the tip of the liver on its outer side, returns on its inner side, and pursues its course then as a single channel under the pharynx, where it is called the ventral aorta. In this region it is contractile, deriving its muscles from the walls of the ventral coelomic tube. Vertical branchial vessels

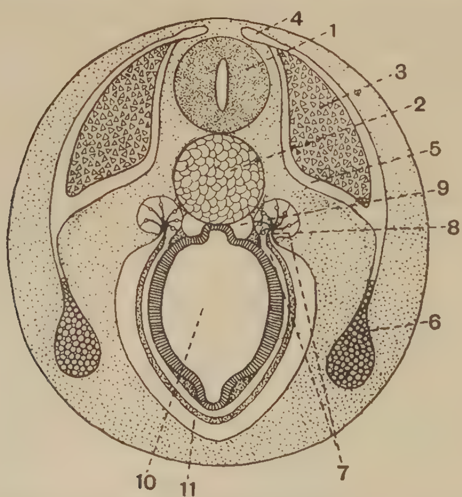


FIG. 198. Diagrammatic transverse section of *Amphioxus* to show the relation of the excretory and genital organs.

1. Nerve-cord. 2. Notochord. 3. Myotome. 4. Upper sclerotome which gives rise to the fin-rays. 5. Lower sclerotome. 6. Developing genital organ. 7. Dorsal coelomic canal crossed by the solenocytes of the nephridium communicating with the branchial coelomic canal in the gill-bar: the lower ref.-line points to the branchial coelomic canal. 8. Nephridium. 9. Dorsal aorta. 10. Pharynx. 11. Atrial cavity.

called arterial arches are given off; these ascend in the gill septa, that is, the portions of the wall of the pharynx intervening between the gill-slits. Arriving at the dorsal line of the pharynx these vessels empty into two longitudinal vessels, the dorsal aortae, which further back unite into one (Figs. 189 and 190). The tongue-bars also contain vessels emptying into the dorsal aortae; these communicate with the branchial vessels through what are called synapticulae, that is, cross pieces tying the tongue-bar to both sides of the gill-slit which it divides (Fig. 191).

There is also a well-marked blood-vessel running along the inner side of the genital organs on each side of the animal. These vessels are connected with the subintestinal vein where it runs along the liver by a series of transverse branches carried in folds crossing the atrial cavity. These longitudinal veins have been compared to the cardinal veins of the fishes (see p. 433) and the strongest pair of transverse vessels to the ductus Cuvieri (see p. 433).

Both gill-bar and tongue-bar are strengthened with rods of gelatinous tissue. These are the precursors of the visceral arches, which form such an important part of the skeleton in the higher Vertebrata. There are two sheaths surrounding the notochord, an inner primary one which is produced by the cells of the notochord itself, and an outer which is deposited round a hollow outgrowth from the myotome called the lower sclerotome (5, Fig. 198). This outer sheath surrounds not only the notochord but also the nerve-cord. From it are given off the myocommata, i.e. fibrous septa which divide one myotome from the next. The upper sclerotomes are the cavities in the dorsal fin-fold mentioned on p. 400.

The reproductive organs are very simple in construction. The sexes are separate, and ovaries and testes closely resemble each other in external appearance (Fig. 197). They take the form of squarish masses, which are surrounded by cavities termed gonadic pouches, embedded in the outer walls of the atrial cavity. When ripe, eggs and sperm are dehisced into the gonadic pouches. Then they escape by pores which are formed at sexual maturity into the atrial cavity, thence to the exterior through the atrial pore. The fertilised egg develops into a free-swimming larva of a remarkable form. There are no atrial folds covering the gills, but one set of slits is developed long before the other, and the mouth appears on the left side. It has been proved that the sexual organs are outgrowths from the lower ends of the myotomes, and remain for some time connected with these by strings of cells (Fig. 198).

The Hemichorda and Cephalochorda are found all over the tropical and temperate regions of the world wherever a suitable substratum is found. The Hemichorda burrow in mud rich in decaying matter, but the Cephalochorda prefer clean sand, their food as we have seen consisting of swimming organisms.

Sub-phylum III. TUNICATA or UROCHORDA.

By many the group of Tunicata or Urochorda would be considered the lowest portion of the phylum Vertebrata, and if we had regard only to the adult structure this could not well be denied, for in the adult hardly a trace of the Vertebrate relationship is discernible. But the Tunicate commences life as a larva showing a more developed structure in several important points than *Amphioxus* possesses at any period of its life-history, and hence we must regard the simple organisation of the adult as a degraded rather than a primitive condition of affairs.

Larva. The typical Tunicate larva is often called a tadpole because its form recalls that of the well-known larva of the frog. It attains a length of about a quarter of an inch, and consists of a small round trunk and a thin vertical tail four or five times as long as the trunk. The tail is the organ of locomotion, and is provided with a sheet of muscles on either side by the alternate contraction of which powerful side-strokes are executed and the animal is propelled forward (13, Fig. 200). The tail is stiffened by a well-developed notochord—which does not extend into the trunk, hence the name "Urochorda" (Gr. οὐρά, tail; χορδή, a string). A uniform flap of skin, a continuous fin, forms a border to the tail. The trunk contains the enlarged pharynx which opens by a narrow mouth in front: and laterally communicates with the exterior by two ciliated openings—the gill-slits. Its ventral wall is swollen out into a pocket which causes the under lip to protrude as a bulky chin. In this pocket we find developed a ciliated groove, the endostyle, having the same position as the organ similarly named in *Amphioxus*. On the chin outside are three peculiar warts which secrete a sticky slime and which are used by the larva to fix itself to surrounding objects. The pharynx leads behind into a short intestine which is attached to the ectoderm high up on the side far in advance of the root of the tail. Hence the process of shifting forward the anus and the corresponding development of a purely muscular tail have been carried much further in this tadpole than in *Amphioxus*.

The nervous system in the tail is a simple neural tube; but in the trunk it expands into a thin walled vesicle, the so-called sense-vesicle, which is the representative of the cerebral vesicle of *Amphioxus* and the forerunner of the fore-brain of the higher Vertebrata. As in the larva of *Amphioxus*, the sense-vesicle opens to the exterior,

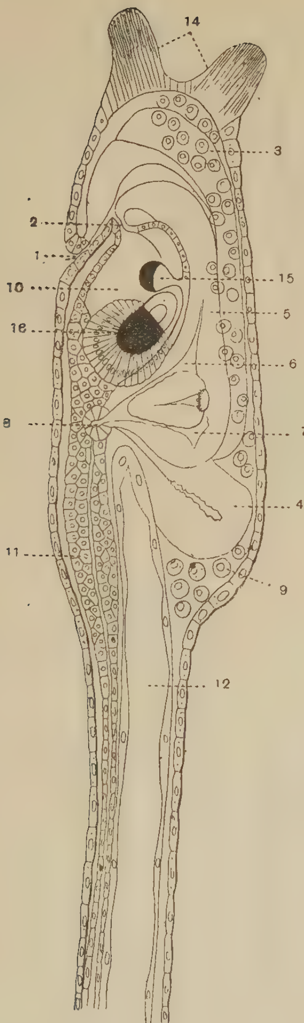


FIG. 199.

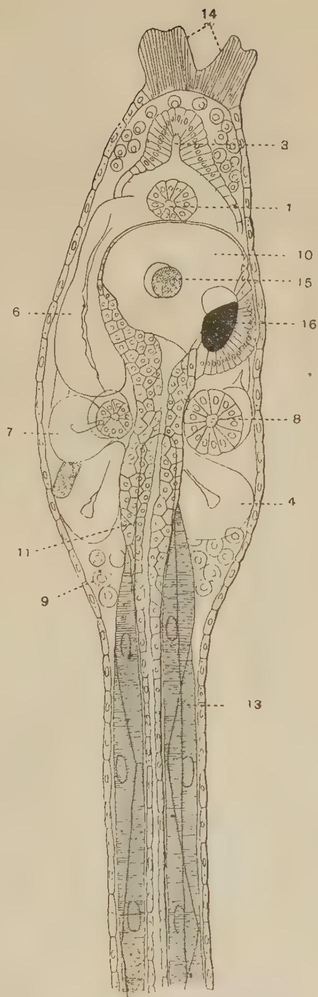


FIG. 200.

FIG. 199. Side view of the anterior end of a larva of *Ascidia* which has been free-swimming for two days × 375. FIG. 200. Dorsal view of the same. After Kowalewsky.

1. Mouth. 2. The connection of the brain with the stomodaeum. 3. Endostyle. 4. Intestine. 5. Branchial cavity. 6. 1st gill-slit. 7. 2nd gill-slit. 8. Atrial opening. 9. Blood corpuscles. 10. Cavity of brain. 11. Dorsal nerve-tube. 12. Notochord. 13. Muscles. 14. Fixing organs. 15. Otolith. 16. Eye.

but the spot where this occurs is involved in the invagination which forms the stomodaeum. The tube connecting the sense-vesicle and the stomodaeum is called the neuropore (2, Fig. 199). Part of the side-wall of this vesicle is modified so as to form a cup-shaped eye with a simple cuticular lens directed inwards. From the floor rises a pillar of cells on which a ball of calcareous matter is balanced; this acts as an otolith, and the whole forms a rudimentary ear.

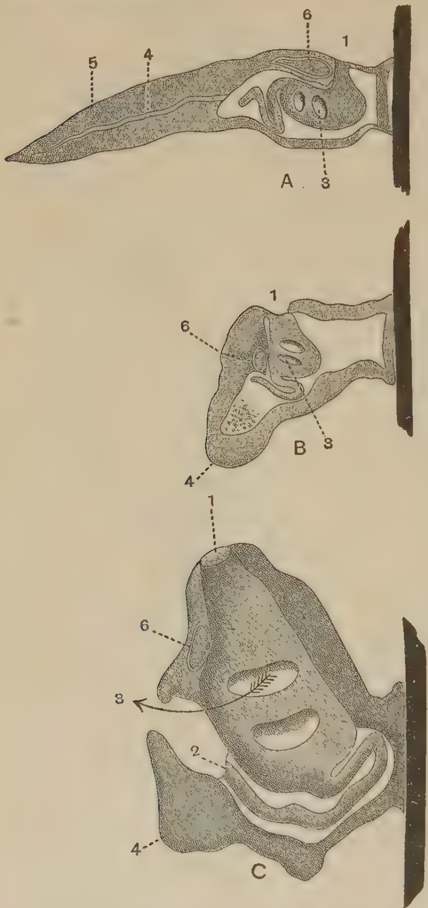


Fig. 201. Diagram of the fixing and changes undergone by a larval *Ascidian*. From Lankester.

1. Mouth. 2. Anus. 3. Gill-slits. 4. In A, notochord; in B and C, vanishing tail. 5. In A, tail. 6. Brain.

Thus both in the structure of the nervous system and the position of the anus, the tadpole of Tunicata is more advanced than the *Amphioxus*.

Although, as we have seen, both mouth and anus are present, yet they cannot be used, for they are closed by a sheet of gelatinous matter. This is the test which is secreted by the ectoderm cells and envelops the whole body, so that during its brief free-swimming life the Ascidian takes no food.

Metamorphosis.

After swimming for a short time the larva fixes itself by its chin-warts to a suitable substratum and undergoes a very rapid metamorphosis. The tail shrinks and is absorbed, notochord and nerve-tube disappear: the sense-vesicle also disappears, only its hinder thickened wall persisting as the adult

ganglion (6, Fig. 201). The neuropore however persists and develops into a mass of tubes underlying the ganglion, which is called the sub-neural gland. Its opening acquires a crescentic form with thickened lips, and is called the dorsal tubercle. Meanwhile the chin grows enormously, so as to rotate the mouth up and away from the substratum, and thus the long axis of the pharynx becomes vertical instead of horizontal. The skin of the region where the anus becomes situated is depressed so as to form a groove. This becomes confluent with the outer parts of the two gill-slits, so as to form a single dorsal cavity termed the atrial cavity, the opening of which is not far from the mouth. It must be noticed that this cavity does not correspond to the similarly named cavity in *Amphioxus*: in the case of the last-named animal the atrial walls originate from the dorsal edges of the gill-slits and meet one another beneath the animal; whereas in the Urochorda they arise from the ventral edges of the slits, and are united with one another on the dorsal edge. The gill-slits themselves become changed by the growth of numerous partitions, transverse to the axis of the pharynx, into a series of narrow slits; and then by the formation of another series of stronger bars parallel to the long axis, into a veritable ciliated trellis-work. All this trellis-work is supported by horny rods like the gill-bars of *Amphioxus*. The test thickens enormously and becomes invaded by a finger-like outgrowth

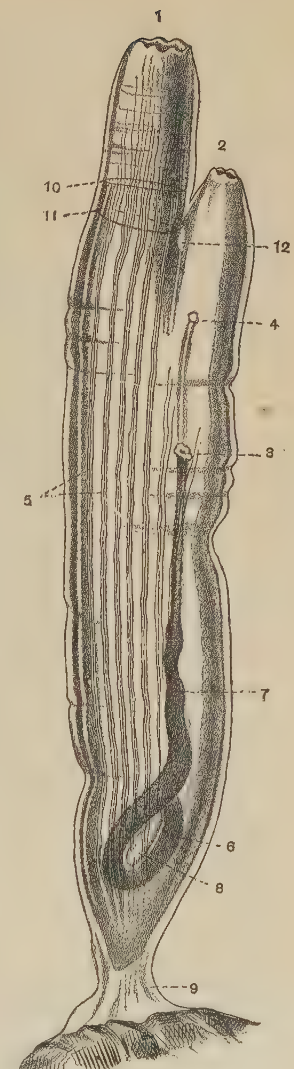


Fig. 202. *Ciona intestinalis* × **1.** The live animal seen in its test; some of the organs can be seen, as the test is semi-transparent.

1. Mouth. 2. Atrial orifice. 3. Anus. 4. Genital pore. 5. Muscles. 6. Stomach. 7. Intestine. 8. Reproductive organs. 9. Stalk attached to a rock. 10. Tentacular ring. 11. Peripharyngeal ring. 12. Brain.

from the hinder part of the body, which carries blood-vessels to it and buds off cells into it which nourish it and change its character. With these changes the adult form is attained. Few would see any resemblance to a Vertebrate in the motionless sac-like body fixed to a stone or rock and looking more like a plant than an animal (Fig. 202).

Structure of adult.

Nevertheless, the Tunicate in some points, even when adult, recalls the structure of *Amphioxus*. Thus we encounter a ring of delicate tentacles a short distance inside the mouth strikingly recalling the velar tentacles of *Amphioxus*. As in that animal also there is a long hypopharyngeal groove or endostyle passing in front into a peripharyngeal band, and secreting a cord of mucus which is worked forward. This mucus is torn into strings by the inrushing current of water and swept backwards to the opening of the oesophagus, entangling in it food particles just as in *Amphioxus*. Instead of a hyperpharyngeal groove, there is a series of tags hanging down from the dorsal wall of the pharynx, called languets. These in life curve round so as to form a row of hooks supporting and directing the mucous strings towards the oesophagus.

The oesophagus leads into a dilated stomach which bends on itself and leads into an intestine which after one or two coils runs forward and opens into the atrial cavity. Its ventral wall is folded inwards, forming a typhlosole similar to that of an Earthworm. As usual the straight terminal portion of the intestine is called the rectum. Near the anus open the ducts of the ovary and testis, for the animals are hermaphrodite. These organs are branched tufts of tubes, the testis being spread over the surface of the stomach, the ovary forming a mass between the stomach and intestine. Oviduct and vas deferens are closely applied to one another, the vas deferens being the more superficial. The latter opens by a rosette of small pores, the ovary by a broad opening, and so the water from the gill-slits, as it passes out of the atrial cavity, sweeps away the sexual cells.

On the ventral side of the pharynx is a V-shaped heart, which is enclosed in a space called the pericardium. The heart is only a specially thickened part of a ventral blood-vessel, which lies immediately under the endostyle and communicates through a network of vessels in the gill trellis-work with the dorsal blood-vessel. Waves of contraction pass over the heart so as to drive the blood forward. After a certain interval the direction of these waves is

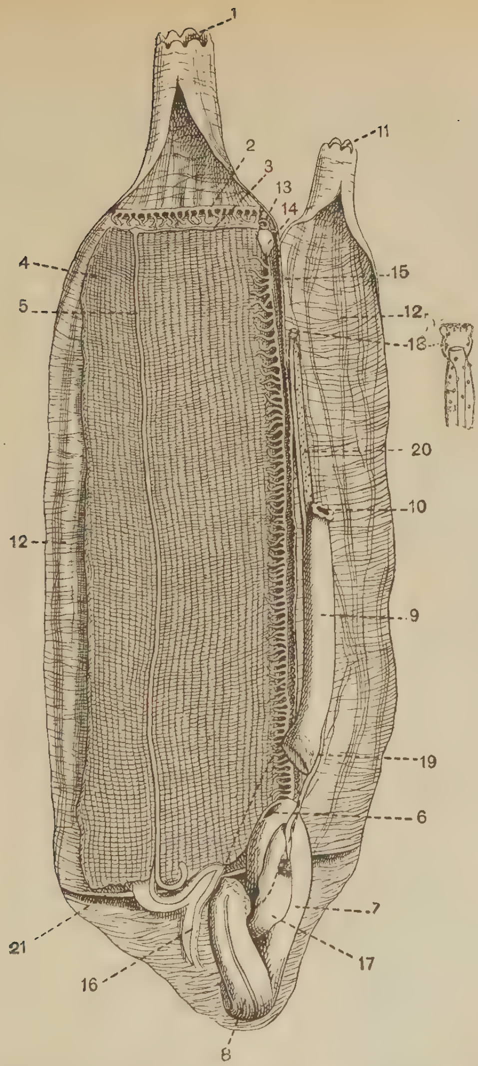


FIG. 203. View of *Ciona intestinalis* lying on its right side. Both the branchial and the atrial cavities have been opened by longitudinal incisions.

1. Mouth. 2. Tentacles. 3. Peripharyngeal groove. 4. Perforated walls of branchial sac. 5. Endostyle. 6. Oesophageal opening leading from the branchial sac to the stomach, rather diagrammatic. 7. Stomach. 8. Intestine showing typhlosole; part of it removed to show subjacent structures. 9. Rectum. 10. Anus. 11. Atrial aperture. 12. Inner surface of mantle showing longitudinal and transverse muscle fibres. 13. Dorsal tubercle. 14. Subneural gland and brain. 15. Cut edge of branchial sac. 16. Heart. 17. Ovary. 18. Pore of vas deferens. The openings of the oviduct and the vas deferens are shown enlarged to the right. 19. Testicular tubes on intestine. 20. Oviduct. 21. Septum shutting off that part of the body-cavity which contains the heart, stomach and generative organs.

reversed, so that the blood alternately goes to the dorsal vessel from the heart and *vice versâ*. With the exception of the heart, however, the blood-vessels do not seem to have definite walls, and must be regarded like those of the Hemichorda as crevices left between various organs.

The sluggish life of the Tunicate has as its only external manifestation the sudden closing of the mouth and atrial cavity by sphincters, and the consequent ejection of water—whence the popular name Sea Squirt. In consequence metabolism is at a low level and not much waste is produced. A good deal of this waste is probably got rid of by the throwing off of the mantle from time to time, but for the rest no definite excretory organ is required. The nitrogenous excretion is stored up as crystals of insoluble uric acid in little vesicles attached to the hinder part of the intestine. These vesicles, together with the cavities of the genital organs and the pericardium, may be looked on as the remnants of the coelom, so that here a similar phenomenon has taken place to what was met with in the case of Arthropods, namely an obliteration of the coelom through the expansion of blood-vessels.

The Tunicata or Urochorda abound on every rocky shore and exhibit a surprising diversity of form. Their principal divisions are as follows.

FIG. 204. Two groups of individuals of *Botryllus violaceus*, after Milne Edwards. Magnified.

1. Mouth opening. 2. Common cloaca of the group.

Class I COPELATA or LARVACEA.

Small forms which retain the larval condition throughout life. The gill-slits are undivided and the anus is ventral. There is no atrial cavity: each of the two gill-slits opens directly to the exterior. The tail is usually carried bent forward at a sharp angle with the body. A temporary test devoid of blood-vessels is found: the animal when disturbed wriggles out of it and forms another.

Class II. The Acopa.

Forms which have lost the tail with its nerves and muscles. These are divided into

Order I. The **Ascidiacea**, fixed forms.

Order II. The **Thaliacea**, which have secondarily acquired the power of swimming by contractions of the whole body carried out by transverse bands of muscle.

The Ascidiacea constitute the great bulk of the Urochorda. Some of them, such as the form taken as a type in the general description given above, remain solitary throughout life, but others bud and form colonies embedded in a common test; these are called Compound Ascidians. But the group is not a natural one, since budding is carried out in different ways in different families, and has therefore probably originated several times. The commonest method is by the outgrowth of a hollow finger-shaped process of the pharynx, called a stolon, arising at the hinder end of the endostyle, which becomes divided into pieces, each forming a bud. On the other hand in *Botryllus* a different method is followed, since in this case the buds originate simply as little pockets of the atrial wall of the parent. *Botryllus* is one of the most beautiful colonial forms; in it the buds are arranged in circles; the atrial openings of the members of a circle open into a common pit in

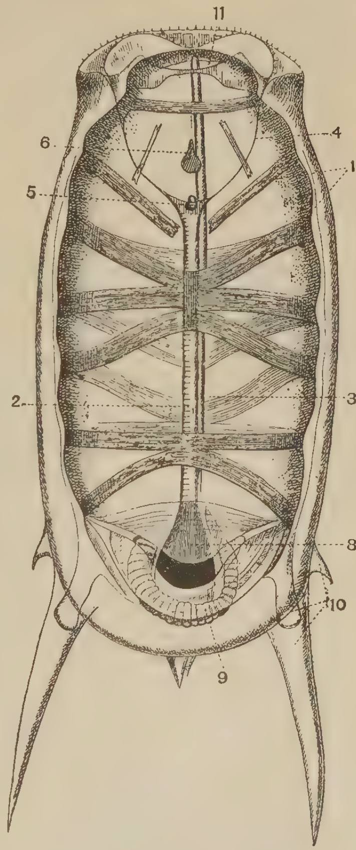


Fig. 205. Dorsal view of a fully-grown specimen of the solitary form of *Salpa democratica* × about 10. From Brooks.

1. Muscle bands. 2. Narrow band representing the dorsal wall of the pharynx, the so-called "gill." 3. Endostyle. 4. Peripharyngeal band. 5. Brain. 6. Ciliated pit. 8. "Nucleus," consisting of stomach, liver, intestine. 9. Stolon or row of young. 10. Processes of mantle. 11. Mouth.

the centre called the cloaca. *Pyrosoma* is a free-floating colonial form, with the shape of a cylinder open at both ends, the atrial cavities of the constituent persons opening on the inner surface, their mouths on the outer. Its name (lit. fire-body) is derived from the circumstance that it is brilliantly phosphorescent.

The Thaliacea are extraordinary forms. They have the shape of cylinders with the mouth at one end and the atrial opening at the other, and their body is surrounded wholly or partly with muscular hoops like the hoops encasing a barrel. The commonest form is *Salpa*, which at intervals may be seen in countless numbers swimming at the surface of the sea. In this

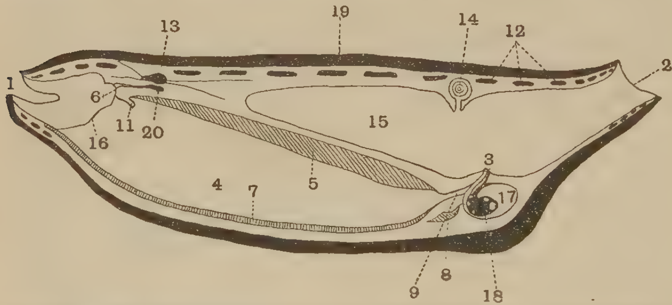


FIG. 206. Semi-diagrammatic view of left side of *Salpa*. From Herdman.
1. Branchial aperture. 2. Atrial aperture. 3. Anus. 4. Branchial sac. 5. "Gill." 6. Subneural gland. 7. Endostyle. 8. Heart. 9. Oesophagus. 11. Languet. 12. Muscle bands. 13. Nerve ganglion. 14. Embryo in ovisac. 15. Peribranchial cavity. 16. Peripharyngeal band. 17. Stomach. 18. Testes. 19. Test. 20. Subneural gland.

animal the test is of a glassy transparency. The two original atrial openings or gill-slits of the larva do not become divided by partitions, but develop into two huge vacuities in the side walls of the pharynx, reducing its dorsal wall to a mere band, the so-called "gill." There are two distinct forms of this animal, a sexual and an asexual, one giving rise to the other, so that here we have a case of "alternation of generations." In the asexual form we find an endostyle-process or stolon which gives rise to a chain of small sexual forms which one by one drop off. Each sexual form produces only one egg. This when fertilised does not give rise to a tailed larva, but becomes attached to the atrial wall of the mother by a knob of maternal tissue containing blood-vessels, called the placenta, which is embedded in a disc of embryonic tissue, through which nourishment diffuses from mother to embryo. In this position the embryo grows up into an asexual form and eventually breaks loose and swims away.

GLOUCESTER

CHAPTER XIX

INTRODUCTION TO SUB-PHYLUM IV, CRANIATA. THE CYCLOSTOMATA

ALL the remaining Vertebrata are distinguished by possessing a skull and brain, and are grouped together as Craniata. The Craniata are separated by a deep gap from the lower forms: but they themselves present a fairly continuous and graded series from the lowest to the highest forms, and their comparative anatomy, especially when we take into account the fossil representatives of the sub-phylum, gives us a fairly good idea of the course which the evolution of Vertebrata has pursued; so much so indeed, that the group might be compared to the fairly reliable and complete records of a country during the historical period, whilst the Hemichorda, Cephalochorda and Urochorda represent the few scattered and scarcely decipherable documents of prehistoric epochs.

Characters.

The Craniata are defined, as we have seen, by the possession of a skull and a brain, though these are only two of the many characters which distinguish them from the other Vertebrata. The skull is composed of either cartilage or bone; and even in cases where the adult skull is completely bony, in the embryo the bone is partly, at any rate, represented by cartilage. Cartilage and bone are really only two peculiar modifications of connective tissue whose fundamental characters it may be useful to recall. There is in every form of connective tissue a gelatinous ground substance traversed by fibres, and applied to these fibres are cells, which are connected with one another by delicate threads of protoplasm and which secrete the greater part of the ground substance and fibres contained therein. In cartilage, the ground substance becomes cheesy in consistence, the fibres being masked, and the cells are arranged by twos and threes in little pockets. These cells are surrounded by concentric layers of dense 'chondrin'

as the cheesy substance is called. These concentric layers make up what is called the capsule of the cartilage cell. When a cartilage cell divides, its daughter cells proceed to form new capsules within the old one and so the main mass of the cartilage is gradually built up. In bone, on the other hand, the cells remain single while the ground substance becomes hardened by depositions of phosphate and carbonate of lime. The spaces occupied by the cells are known as lacunae, and the delicate processes which connect the cells give rise to the capillary canals known as canaliculi in the dried bone, whilst the spaces occupied by blood-vessels traversing the bone are known as Haversian canals.

Primitive skull.

In the simplest form the skull consists of two pairs of pieces of cartilage, one pair of which embrace the front end of the notochord and are termed the parachordals. In front of these is the second pair, termed the trabeculae, which are united behind and before with each other but which diverge in the middle so as to embrace between them the pituitary body, an appendage of the brain. The parachordals develop ridges which wall in the sides of the brain and may form a roof over its hinder portion.

The brain is only the enlarged and modified anterior end of the neural tube, and the existence of a skull-roof is correlated with the presence of neural arches protecting the hinder part of the nervous system. These arches consist of paired pieces of cartilage meeting above the neural tube. They have been shown to be formed as differentiations of solid cellular outgrowths of the myotomes which represent the hollow sclerotomes of *Amphioxus*, and hence it may be that the parachordal part of the cranium at any rate is derived from outgrowths from the walls of the most anterior myotomes which early become fused with one another and otherwise modified.

Haemal arches, which are paired pieces of cartilages with their upper ends implanted in the sheath of the notochord and their outer ends directed downwards, are also always present, and like the neural arches are derivatives of the myotomes. In the region of the tail the haemal arches meet each other so as to form a V beneath the notochord, but in the trunk they simply project out between adjacent myotomes as parapophyses, the ends of which may become movable on the basal parts and are then known as ribs.

Brain.

The brain of all Craniata is sharply divisible into three primary regions called fore-brain, mid-brain and hind-brain (Fig. 207). Of these the first is certainly

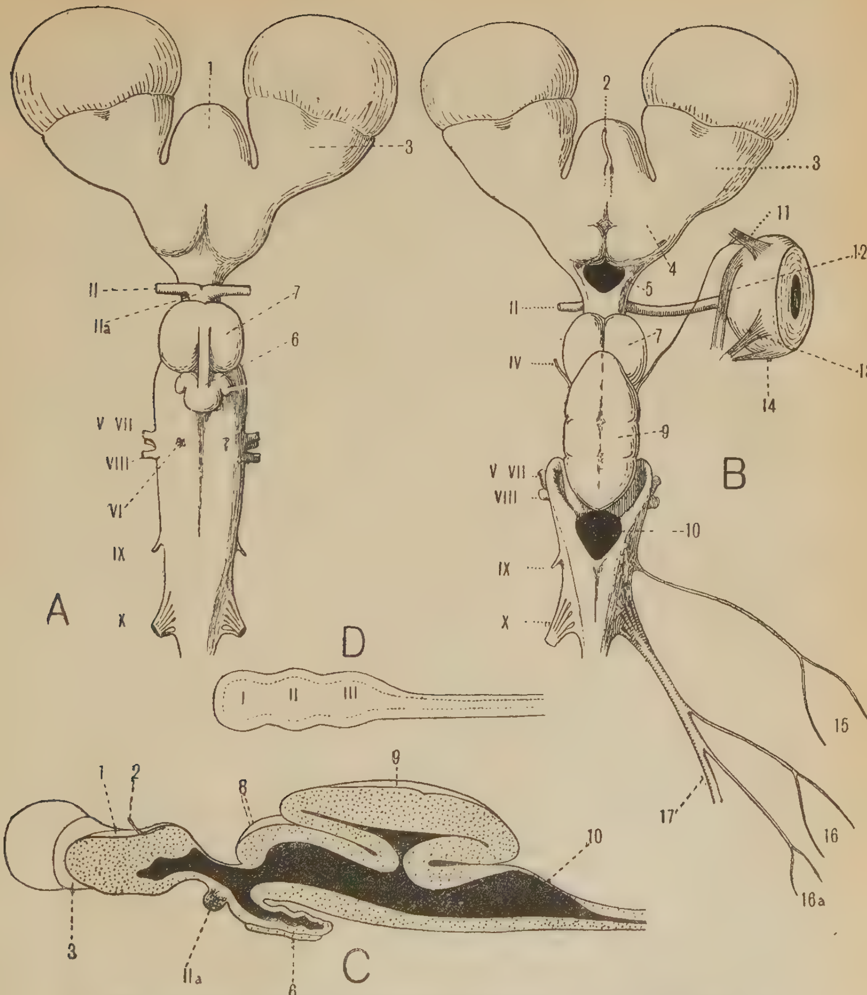


FIG. 207. *Scyllium catulus.* Dissection of the brain and of some of the cranial nerves. A. Ventral view. B. Dorsal view. C. Longitudinal median section. D. Diagram of embryonic brain showing the three primary vesicles.

1. Cerebrum. **2.** Pineal stalk. **3.** Olfactory lobe. **4.** Cerebral hemisphere. **5.** Thalamencephalon. **6.** Pituitary body. **7.** Optic lobes. **8.** Optic lobes. **9.** Cerebellum. **10.** Roof of the hind-brain. **11.** Superior oblique muscle. **12.** Internal rectus muscle. **13.** Superior rectus muscle. **14.** External rectus muscle. **15.** Ninth or glossopharyngeal nerve. **16.** Branch of vagus nerve to second branchial cleft. **16 a.** Branch of vagus nerve to third branchial cleft. **17.** Main trunk of vagus to fourth and fifth gill-slits, to lateral line and to viscera. II. Optic nerve. II a. In A, optic chiasma. IV, V, VI, VII, VIII, IX and X. Roots of fourth to tenth cranial nerves. In D, I, II, III represent the first, second and third primary vesicles of the embryonic brain.

the enlarged and highly developed representative of the sense vesicle of the Urochorda and of the cerebral vesicle of *Amphioxus*. In the embryo it is a simple thin-walled vesicle, the lateral walls of which become changed into the retinae or the essential sensory portion of the eyes. The Craniate eye like that of the Ascidian tadpole, has its perceptive surface turned inwards towards the brain cavity. The nerves by which the eyes are connected with the brain are really the narrowed connections of the lateral portions of the fore-brain with the central portion. The roof of the fore-brain remains thin throughout life and from it a stalk arises leading to a third median eye, the so-called pineal body, vestigial in all living forms. From the front wall of the fore-brain an outgrowth takes place, giving rise to a bilobed vesicle termed the cerebrum, each of the two lobes of which is termed a cerebral hemisphere. This in the higher Craniata is the seat of the more complex mental processes, but in the lower it appears to be intimately connected with the organ of smell. The cerebrum in these cases remains thin-roofed, but its base thickens owing to a great development of nervous matter. In order to distinguish it from the cerebrum the original fore-brain is denoted by the name thalamencephalon for which American authors often substitute the term 'twixt brain.' Underneath this section of the brain lies a glandular organ termed the pituitary body. This body is compounded of a downgrowth of nervous tissue from the fore-brain and of a portion of tissue evaginated and constricted off from the roof of the buccal cavity. It represents the sub-neural gland of the Urochorda, and in the higher Vertebrates produces a substance which is of importance to the normal metabolism of bone and connective tissue, and recent research suggests that its secretion also influences the activity of the kidneys.

The mid-brain acquires thick lateral pouches, the so-called optic lobes: the hind-brain remains thin-roofed, except in front where a transverse nervous band, the cerebellum, is formed. The cerebellum is believed to be the portion of the brain intimately connected with the semicircular canals of the ear (see p. 420) and to have for its function the control of the muscles so as to maintain the equilibrium of the body. The rest of the hind-brain is termed the medulla oblongata or spinal bulb; it controls the beating of the heart, the respiratory movements and other vital processes. The hinder part of the neural tube is known as the spinal cord, and it develops thick walls, so that its cavity is exceedingly small.

The essential element in the nervous system of Vertebrata, as in all other nervous systems, is a kind of cell which has been variously styled nerve-cell, ganglion-cell and neuron. This last name is undoubtedly the best, as it avoids the old misapprehension that regarded the nerve-cell and nerve-fibre as two independent structures.

The minute structure of the nervous system.

On page 62 it was pointed out that the nerve-fibre is a very fine basal outgrowth of a modified ectoderm cell which is the nerve-cell. The cell, including its outgrowth, is termed the neuron. Important discoveries have recently been made on the minute structure of the nervous system of Vertebrata, and we are now able to form a simple and connected idea of the principles on which it is built up. Originating as a simple strip of ectoderm which becomes rolled up so as to form a tube, it is at first composed of cells which extend through its entire thickness and which all abut on the cavity of the tube. Some retain this position but develop branches and deposit a large amount of cuticular substance in their cytoplasm: these, constituting the supporting elements of the system, are termed collectively neuroglia. Other cells retire from the cavity of the tube, becoming more or less rounded in form, but developing a number of outgrowths: these cells are the neurons. Each neuron is provided with a number of branching processes, sometimes arising from a single thick stem; these are called receptive dendrites (Gr. δένδρον, a tree), and they receive impulses. Impulses are transmitted through one long basal process, called the axis-cylinder process or axon, which ends in a tuft of processes often thickened at the tips, which are called terminal dendrites. The name axis-cylinder is suggested by the circumstance that amongst Vertebrata this process is in many cases surrounded by a fatty sheath of a conspicuous white colour, called the myelin; a process with or without this sheath making up what is known as a nerve-fibre. The tuft of dendrites in which the axon ends is found to be in close contiguity either with the receptive dendrites of another neuron, by which means the impulse is transmitted from one neuron to another, or with a gland-cell which is thereby caused to secrete, or else with the muscle-plate of a muscle-fibre, by which means the fibre is stimulated. The muscle-plate is a disc of protoplasm with several nuclei situated at the side of the muscle-fibre. The axon may give off several branches termed collaterals. These like the main stem end in tufts of dendrites; in this way an impulse may spread over several paths. The receptive dendrites of a neuron

may also receive impulses from the terminal tufts of several axons, and in this way impulses are co-ordinated and combined.

As mentioned above, the skull and brain are by no means the only characters which distinguish the Craniata from other Chordata. Perhaps the next in importance is the possession of three well-developed pairs of sense-organs, nose, eyes and ears.

Sense-organs.

Of these the nose is the most simply constructed. It consists merely of a pair of pits in the skin at the most anterior portion of the body, the lining of which develops ridges covered with sensory cells, having an olfactory function

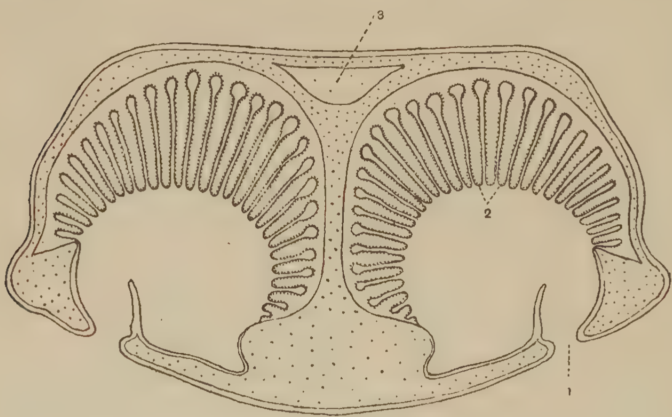


FIG. 208. Transverse section through the snout of a Dogfish, *Scyllium canicula*, to show the structure of the nose × 2.

1. Opening of olfactory sac. 2. Olfactory epithelium. 3. Ethmoidal region of the cartilaginous skull.

(Fig. 208). The essential element in all sense-organs is the sense-cell, which generally resembles the neuron in possessing a basal process terminating in a tuft of dendrites by which the stimulus is transmitted as an impulse through a neuron, for in Craniata a sense-cell is never in direct communication with a muscle-fibre. Where the basal process is absent the body of the sense-cell itself is enwrapped by the branching receptive dendrites of a neuron beneath it. An olfactory sense-cell differs from a neuron in possessing one or more stiff peripheral processes projecting from the surface of the body, by which stimuli are received from the external world. These are termed s e n s e - h a i r s, and they are excessively delicate in structure. Sense-cells are never combined by themselves into an epithelium: they are always intermixed with stiff supporting cells

which usually have at the base several root-like branches. The front end of the brain comes in direct contact with the wall of the nasal sac and the axons of the sensory cells stretch into the brain, thus constituting the olfactory nerve (Fig. 207).

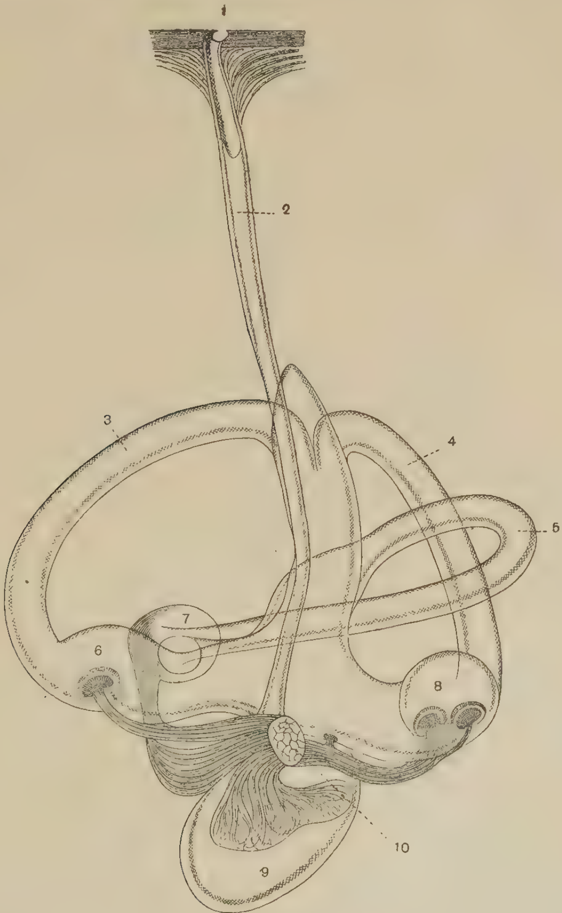


FIG. 209. Ear of *Chimaera monstrosa* L. × about 4. From Retzius. Seen from the inner side.

1. External aperture on roof of skull. The wall of 2, the "ductus endolymphaticus," is partly removed to show that it is a tube. 3. Anterior, 4, posterior, and 5, horizontal semicircular canals. 6. Anterior, 7, external, and 8, posterior ampullae. 9. Sacculus. 10. Auditory or 8th nerve.

The ears are also at first pits of the skin placed further back at the sides of the hind-brain. In the lower forms these pits retain a

narrow connection with the exterior throughout life through a long tube called the ductus endolymphaticus (2, Fig. 209). In the higher forms this tube is still recognisable but no longer opens to the exterior. Each pit contains a watery fluid termed endolymph and becomes constricted in the middle into an upper portion, the utriculus, and a lower portion, the sacculus. In all Craniata except the Cyclostomata the former gives rise to three flat outgrowths placed in planes at right angles to one another (Fig. 209). These outgrowths become converted into half-rings by the meeting of their walls in the middle of each, and in this way three semicircular canals are formed, called respectively anterior, posterior, and horizontal. The primary function of the whole organ, like that of the otocysts of Medusae, Crustacea and Mollusca, is to enable

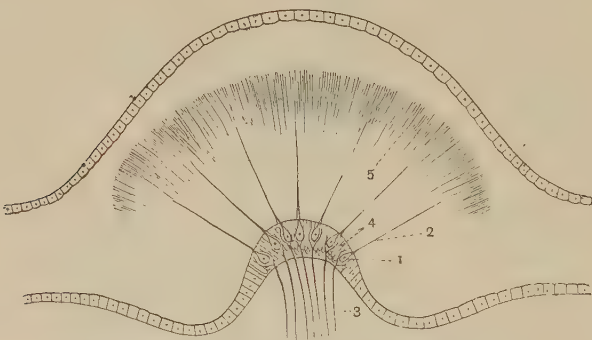


FIG. 210. Section of ampulla of the internal ear.

1 Sense-cell bearing a long hair. 2. Sense-hair. 3. Nerve termination branching round base of sense-cell (dendrites of a deeply placed neuron). 4. Interstitial cell. 5. Gelatinous cup in which the sense-hairs are embedded.

the animal to perceive its position. Where each semicircular canal arises from the utriculus it is swollen, and the swelling is termed an ampulla. The wall of each ampulla projects inwards, and the projection contains cells with exceedingly long sense-hairs which project into the cavity of the ampulla (Fig. 210). The free ends of these hairs are embedded in a gelatinous cup which sways about with the motion of the endolymph and thus stimulates the sense-cells of the ampulla pressing on their sense-hairs as on levers. It can be thus seen that the whole organ is admirably adapted to record change of position in any direction, since any change of position can be completely analysed into movements in three planes. The lower part of the organ or

sacculus has cells adapted to be stimulated by vibrations in the surrounding lymph. It often contains calcareous "ear-stones." In higher forms it gives off a spiral tube, the cochlea, which contains the true auditory sense-cells. These form the organ of Corti (see p. 648) a more complex structure than the sensory epithelium of the sacculus and ampullae, but resembling it in consisting of hair-cells—the bases of which are embraced by the receptive dendrites of neurons. The groups of neurons which are in relation to all these sensory structures form the several auditory ganglia. Both nose and ear have cartilaginous or bony coats which become firmly connected with the skull; these are known as the sense-capsules.

The eye is the most complicated, and in the higher Craniata by far the most important, of the sense-organs. In its origin, as we have seen, it is the lateral portion of the fore-brain which when constricted off is known as the primary optic vesicle (Fig. 211). The outer wall of this becomes modified into a sensory epithelium called the retina. This consists of a row of visual cells, their free ends directed inward towards the brain and produced into the characteristic striated rods. Beneath these sense-cells there are two layers of neurons, the dendrites of which, mingling with the dendrites of the sensory cells, give rise to a comparatively thick bed of nervous tissue. Long, however, before the sense-cells are developed, the primary vesicle of the eye has completely altered its shape. The outer wall has become pushed in on the inner so as to completely reverse the shape of the sac (Fig. 211). Its cavity is reduced to a mere slit, and its takes on the form of a very deep double cup with its concavity directed outwards. This is the cavity of the eyeball

FIG. 211. Transverse section through a third day Chick to show origin of the retina from the brain and of the lens from the ectoderm. Highly magnified.

1. Cavity of brain. 2. Outer layer of retina surrounding the black, thicker layer which will form the rods and cones. 3. Lens arising as a hollow invagination. 4. Pineal body originating. 5. Embryonic connective tissue.

or so-called secondary optic vesicle, the clear gelatinous connective tissue inside which is known as the vitreous humour. The connective tissue surrounding the vesicle peripherally forms a tough fibrous or even cartilaginous capsule called the sclerotic coat, lined by a thin vascular tissue, the choroid coat. The sensitive and nervous outer layer of the primary vesicle is known as the retina, the other layer (which becomes loaded with pigment) as the pigment epithelium of the retina. If we analyse the structure of the retina, we find that it has fundamentally the same structure as the central nervous system of which, as its origin shows, it is really a part. Thus there are a number of branched and cuticularised supporting cells called fibres of Müller, extending throughout the whole thickness of the retina, and the main mass of the retina is made up of neurons. There is, however, in addition a layer of characteristic visual cells; that is to say, of sense-cells, with a comparatively thick striated rod in place of the ordinary sense-hair. Visual rods have already been described in the eyes of Anthomedusae (p. 64) and of Arthropoda (p. 197); they occur wherever the capacity for vision is developed. In the retina of Craniata there are two varieties of visual cell, called respectively rod-cells and cone-cells. In the first, the visual rod is narrow and cylindrical, and the body of the cell beneath is filamentous with a rounded swelling for the nucleus; the basal process ends in an unbranched knob, that is to say, in a single dendrite. In the cone-cell the rod is conical with a broad base, to which the body of the cell containing the nucleus is immediately applied; the basal process ends in the normal manner in a tuft of dendrites. The basal processes of both kinds of sense-cell are in close relation to the receptive dendrites of a layer of neurons with small cell bodies; the axis-cylinder processes of these in turn end close to the receptive dendrites of a layer of neurons with large cell bodies situated close to the outer basal surface of the retina, which give rise to the fibres constituting the optic nerve. Taking a general view therefore we may say that the retina is a sensory nervous epithelium consisting of a layer of sense-cells underlaid by two layers of neurons. Before its structure was thoroughly understood, however, the appearance of the retina in transverse section was a bewildering mass of fibres and nuclei, in which for descriptive purposes different layers were distinguished. These, reckoning them in the order proceeding from the inner side of the eyeball towards the lens, were as follows:—(*a*) the layer of rods and

cones, (*b*) the outer nuclear layer (VI, Fig. 212) consisting of the bodies of the visual cells containing their nuclei; (*c*) the outer molecular layer (V, Fig. 212) consisting of sections of the basal processes of the visual cells and of the receptive dendrites of the neurons with small cell bodies; (*d*) the inner nuclear layer (IV, Fig. 212) consisting of the bodies of the above neurons; (*e*) the inner molecular layer (III, Fig. 212) consisting of sections of the basal processes of the above neurons and of the receptive dendrites of the

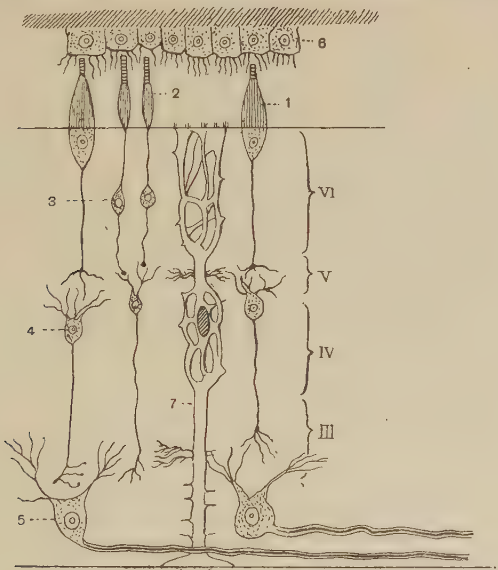


Fig. 212. Diagram to illustrate structure of a retina. The several "layers" are indicated by the numerals III, etc. in order from within (vitreous humour) outwards.

1. Cone. 2. Rod. 3. Nucleus of rod-cell. 4. Small neuron. 5. Large neuron. 6. Pigment epithelium. 7. Fibre of Müller or a supporting cell.

neurons with large cell bodies; (*f*) the layer of nerve-cells consisting of the bodies of the last-named neurons; and finally (*g*) the layer of nerve-fibres consisting of the basal processes of the last-named neurons which constitute the optic nerve.

The remainder of the eye is to be looked on as a part of the skin of the side of the head which has been rendered transparent in order to allow light to reach the retina. It consists of a lens and cornea, separated by a chamber containing the aqueous humour. The lens is an originally hollow plug of ectoderm cells,

which breaks loose from the skin and lies in the mouth of the secondary optic vesicle (Fig. 211). The skin outside the lens forms the cornea, which is transparent. The cornea is joined to the edges of the sclerotic capsule and thus completes the boundary of the eye-ball, as the fully-elaborated sense-organ may be termed. If the above description has been followed it will be seen that in a Craniate light must reach the visual cells through their basal and not through their visual ends. As this is contrary to the almost universal rule obtaining throughout the animal kingdom, we cannot believe it to be a primitive arrangement. Rather we must believe that when the eye was being evolved the rods of the visual cells were directed towards the light, and that the epithelium of which they form a part was exposed and not rolled up into a neural tube; in a word, that the front portion of the nervous system of Vertebrata at any rate was once a plate of sensitive skin. It is most suggestive to note that in the larva of the Hemichorda we find such a plate with two eye-spots at the apex of the prae-oral lobe.

Skin.

The external layer of the skin or ectoderm of Craniata is quite peculiar in the animal kingdom, in that it consists not of one, but of many layers of cells. On closer inspection, however, it is seen that the deepest layer, consisting of columnar cells alone, really represents the ectoderm of the other phyla. This layer instead of becoming directly converted into cuticular substance externally, as, for example, in the Arthropoda, buds off layers of cells from its outer surface which, as they become pushed further and further out, become bodily converted into horny matter and scale off. The ectoderm rests on a specially firm bed of connective tissue called the dermis.

Nerves.

A very peculiar feature in the Craniata is the character of the scattered sense-cells of the skin. These end in sense filaments embedded in the ectoderm, not projecting beyond it. These filaments have however grown enormously, and with their growth the bodies of the cells with the nuclei have come to lie deep down in the body and so have become quite indistinguishable from ordinary neurons. Here they form metamerically arranged packets of cells lying at the side of the nerve-cord and known as the spinal ganglia. They are connected with the nerve-cord by their basal outgrowths or nerve-tails, which constitute the dorsal roots of the spinal nerves corresponding to the dorsal sensory nerves of *Amphioxus*. To each myotome a motor nerve is given off, as in *Amphioxus*, but in the Craniates the fibres of this nerve are

bound up a certain distance with the long peripheral processes of the sense-cells which constitute the spinal ganglia, so as to form a compound sensory-motor nerve, which is then said to have a *dorsal sensory* and a *ventral motor root*.

In Craniata there exist below the spinal ganglia another series termed the *sympathetic* ganglia. These ganglia retain their connection with the spinal cord by nerves called the *rami communicantes*, and from them there are given off motor nerves to the smooth visceral muscles encircling the blood-vessels. Successive sympathetic ganglia are connected by a longitudinal commissure, and so there is a chain of sympathetic ganglia on each side of the spinal cord. The purpose of this commissure seems to be to distribute the nervous impulse proceeding from the spinal cord over a considerable area and to prevent too acute a contraction occurring in any one part of a blood-vessel. They must be regarded as portions separated from the ventral or motor part of the spinal cord.

In the higher Craniata another series of ganglia (the *visceral ganglia*) are situated on the mesentery. These are connected with the sympathetic ganglia and send nerves to the muscles of the gut, the peristalsis of which they control. It is usual to reckon ten pairs of nerves as appertaining to the brain. The *first* or *olfactory* pair are formed by a large number of nerve fibres connecting the olfactory lobes of the brain with the epithelium of the nasal sacs (Fig. 207). The second or optic nerve is formed by nerve-fibres growing along the stalk uniting the primary optic vesicle with the brain (Fig. 211). The nerve fibrils which run in this stalk go mainly but not entirely to the opposite side of the brain, each side of the brain receiving impulses from both eyes. Thus in the floor of the thalamencephalon, or primitive fore-brain, there is a crossing of fibres proceeding from the two eyes. This part of the floor becomes nipped off by grooves from the rest, and is known as the *optic chiasma*. The chiasma is connected with the combination of the stimuli received by the two eyes so as to produce a reflex impulse which is transmitted to the eye-muscles and causes them to direct both eyes towards the same point of the compass and thus to be focused on the same object. In people who squint the over development of one of the muscles of one eye prevents this purpose being attained. The *third* or *motor oculi*, the *fourth* or *patheticus*, and the *sixth* or *abducens* nerves are motor nerves, supplying the eye muscles derived from the head cavity, the mandibular cavity and the first myotome respectively (see p. 437).

The fifth or trigeminal, and seventh or facial, are most interesting nerves, being sensory as well as motor. The sense-organs which are supplied by the seventh nerve in the lower Craniata are peculiar. These organs are scattered over the prae-oral part of the body or snout and the sides of the head, and are known as the mucous canals. On the snout they have the shape of deep tubes swelling out at the bottom into sacs or ampullae; and on the head, of canals communicating at intervals with the exterior by vertical tubes. Certain of the cells lining these tubes develop blunt, freely projecting sense-hairs, recalling the character of the auditory cells, whilst others secrete the mucus with which the tubes are filled and whence they derive their name. It is probable that the function of these organs is somewhat allied to that of the ear, i.e. perception of vibrations, for it has been proved that a fish deprived of its eyes is still able to guide itself along tortuous passages so long as this organ remains intact, and this is explicable only on the assumption that the reflected pulses of the water are felt by these organs. The branches of the seventh nerve which supply them are known as (*a*) the ophthalmic branch which runs above the eye, (*b*) the buccal branch which runs along the roof of the mouth beneath the eye, and (*c*) the hyomandibular which runs vertically downwards behind the eye and in front of the first functional gill-slit. The eighth or auditory cranial nerve goes to the ear, and arises in such close proximity to the seventh that it may be regarded as a specialised branch of it, the ear itself being very possibly a highly specialised mucous canal.

The fifth nerve supplies a series of peculiar sense-organs known as end-buds. These have the form as their name implies of a bud-like aggregation of cells, consisting of supporting cells intermixed with sense-cells with short fine sense-hairs. These end-buds are scattered over the bodies of many fish and are supplied by sensory branches of the fifth nerve. In other Craniata they are confined to the interior of the buccal cavity and subserve the function of taste. The so-called ophthalmic branch of the fifth nerve runs over the eye closely parallel to the similarly named branch of the seventh but its fibres go to end-buds and to unspecialized endings in the skin not mucous canals. The other divisions of the fifth and seventh are distributed to the region of the mouth and to that of the first gill-slit respectively. They both fork; the upper branch of the fifth goes to the upper jaw and the lower to the lower jaw, while one branch of the seventh passes in front and the other behind the

spiracle. The ninth or glossopharyngeal nerve is similarly forked round the first true gill-slit (Fig. 207).

The tenth or vagus or pneumogastric nerve, which is certainly a compound one, gives off a branch to each of the remaining slits, to which it bears a relation similar to that borne by the ninth nerve to the second slit. The main stem of the nerve passes along the alimentary canal and sends nerves to its muscles and to those of the heart, all these muscles being developments of the inner or splanchnic wall of the unsegmented coelom. The tenth nerve has also in the lower Craniata a sensory division. This separates from it soon after it leaves the brain and passes backward, supplying a series of long mucous canals fused together, called the lateral line, which extends from head to tail along the mid-lateral portion of the body and is provided with a series of openings to the exterior. In some forms this sensory branch, the so-called lateralis, appears to originate from the brain as an independent nerve and in all cases its constituent fibres can be traced back through brain substance to a peculiar group of neurons in the side of the hind-brain known as the tuber acusticum. From this same group the eighth nerve and the sensory branches of the seventh nerve take their origin. On account of its extensive area of distribution the tenth nerve has received the name of vagus (wandering).

Alimentary canal.

The alimentary canal exhibits a marked difference from the condition found in the lower Chordata. The gill-slits are reduced in number, there being as a rule not more than eight; it would indeed be more correct to speak of them as gill-pouches. In this respect Craniata agree with the Hemichorda in contrast to the Cephalochorda and Urochorda. No trace of a tongue-bar has however been found in any Craniate.

The endostyle becomes shut off from the pharynx and thus loses entirely its original function; it branches and forms a mass called the thyroid gland. The evil results attendant on its removal or diseased condition and experiments on living animals show that it secretes into the system a substance which has a beneficial influence on metabolism, especially as regards the "tone" of the nervous system and the growth of connective tissue.

The subneural gland of the Urochorda, on the other hand, seems to be represented by a structure called the pituitary body. This, like the subneural gland, is a dorsal pocket of the stomodaeum, but it becomes cut off from all connection with the mouth and

intimately associated with a downgrowth of the brain, called the infundibulum, to form an organ having an influence on the well-being of the animal (see p. 416). Since in the case of the Urochorda the subneural gland is fashioned out of the persistent communication of the sense vesicle with the exterior, one is tempted to regard the close connection of the infundibulum and the pituitary body as remnants of the former connection of the brain and stomodaeum in the ancestors of the Craniata. Some authors maintain that a rudiment of the infundibulum is to be seen even in the cerebral vesicle of *Amphioxus* (see Fig. 193).

Except in the lowest forms the alimentary canal is differentiated into several well-marked divisions. There is to begin with a stomodaeum called the buccal cavity lined by an epithelium consisting of many layers similar to that forming the epidermis. The first division of the endodermal tube is called the pharynx, and into this the gill-slits open. Following on the pharynx is a tube of narrow diameter, termed the oesophagus or gullet, which leads into the stomach. The line of demarcation between ectoderm and endoderm is entirely obliterated in the adult, since the epithelium lining both pharynx and oesophagus is many layered. The stomach consists of the first of the loops into which the alimentary canal is bent in consequence of its being longer than the body; it is a greatly dilated portion of the canal and in it the food is stored until a large amount of digestion is accomplished. As in other animals, the food is moved from place to place by peristaltic contractions of the visceral muscles derived from the inner wall of the coelom. There is a particularly powerful girdle of these called the pyloric sphincter, which by remaining contracted keep the distal end of the stomach, the so-called pylorus, closed until the work of digestion is accomplished, when they relax and allow the food to pass on into the next division of the canal, the intestine. The walls of the proximal part of the stomach are produced into small pouches, termed the gastric glands, the cells lining which secrete a substance called pepsin, which has the power of turning the proteid of the food into soluble peptone.

Pepsin is an example of the class of substances known as digestive ferments or enzymes: these are complex substances of unknown constitution which have the power of effecting a large amount of chemical change without themselves undergoing a permanent alteration. The object of their action on food-stuffs is to render them soluble, and therefore fitted for absorption by the

wall of the canal. Pepsin is active only in an acid medium, and free hydrochloric acid is found in the contents of the stomach in small quantities, produced by special cells in the walls of the pouches just mentioned.

An organ called the liver is very conspicuous (Fig. 226). It consists of a ventral outgrowth of the gut, arising just behind the stomach, which extends forwards and branches into an immense tree-like mass of tubes welded together by connective tissue into a solid mass extending forwards and nearly obliterating the front part of the body cavity. The branches of the tree unite with one another in such a way as to constitute a network of rods of cells. Whether this organ really performs the same function as the so-called liver in *Amphioxus* is doubtful. It has been proved that the function of the Craniate liver is largely the elaboration of an alkaline fluid called the bile. This is partly excretory in nature, but has an important influence upon the processes of digestion and absorption in the intestine. It neutralises the acid of the stomach and causes the food when it enters the intestine to be alkaline. The main stem of the liver tubes is called the bile-duct; there is often a lateral outgrowth from this which acts as a reservoir for the bile, called the gall-bladder. Besides this, the liver cells can extract from the blood with which they are bathed, sugar and convert it into a substance called glycogen, which is allied to starch in composition, and which acts as a reserve of carbohydrate material available for the system as needed. Among other influences which the liver exercises on the chemical processes of the body is the very important one of transforming the nitrogenous waste products into a suitable form (urea or uric acid) for excretion by the kidneys.

Another outgrowth from the intestine arises sometimes just behind the opening of the bile-duct, sometimes from the duct itself. This outgrowth, like the liver, branches into a tree of tubes which are bound together by connective tissue to form a solid mass, though one of much smaller size than the liver. This organ is called the pancreas and it produces a secretion called pancreatic juice, by which the process of digestion is completed. This juice contains three ferments: these are amylopsin, which converts starch into soluble sugar; trypsin, which, acting only in an alkaline medium, converts proteid into peptone and simpler derivatives; and steapsin, which splits up fat into soluble fatty acids and glycerine. The fatty acids unite with the alkalis present in the mixed contents of the intestine to form soluble soaps, and

these are absorbed along with the glycerine, a reconstruction into fat taking place in the intestinal epithelium.

Intermixed with the tubules of the pancreas are groups of cells known as the islets of Langerhans. These pour some substance into the blood which enables the sugar, which is one of the principal products of digestion, to be combined with other substances so as to build up protoplasm. When the pancreas is attacked by disease, and the "islets of Langerhans" destroyed, a malady known as diabetes sets in. This is a discharge of large quantities of sugar through the excretory organ accompanied by a wasting of the tissues which leads to death.

The intestine is always somewhat longer than the body. Hence it must be to some extent looped or twisted (Fig. 226), though this may express itself only in a slight curvature. A fold projecting into it in some forms represents the typhlosole of the Urochorda and is known as the spiral valve, since it shares in the twisting. In the intestine the digested food is absorbed and transferred to the blood-vessels and lymph-canals. The last portion of the intestine is usually of larger diameter than the rest and is called, when thus distinguishable, the large intestine. In it the indigestible material is elaborated into faeces for expulsion by the anus.

Circulatory system.

The blood system of the Craniate is distinguished by the possession of a large and well-developed heart, which, like the heart of the Urochorda, is an enlargement and specialisation of part of the ventral vessel. The space in which it apparently lies—really, into which it protrudes,—is called the pericardium, and is only an anterior part of the coelom shut off from the rest by the development of a transverse septum. The heart is constricted into four chambers, becoming successively more thick-walled as we proceed forwards, and named, beginning from behind, the sinus venosus, the atrium, the ventricle and the conus arteriosus (Fig. 214). It is bent into an S-shape, so that the sinus venosus is dorsal and posterior, the atrium dorsal and anterior, the ventricle ventral and posterior, and the conus arteriosus ventral and anterior. The conus arteriosus leads into the ventral aorta, which gives off the arterial arches; these are branches which in the lower Craniates ascend between the gill-sacs and ramify on their walls. From the gills the blood collects into epibranchial vessels which join to form two longitudinal vessels on the dorsal wall of the pharynx, the roots of the dorsal aorta. These unite behind the pharynx into a single dorsal aorta, giving blood to all

the hinder part of the body. The forward extensions of the two longitudinal vessels carry blood to the head and are known as the carotid arteries. There can be little doubt that the impulse leading to the evolution of the heart came from the necessity of having a strong force to drive the blood through the capillary channels on the walls of the gill-sacs.

In the embryos of all Craniates the number of these paired connections between the ventral aorta and the roots of the dorsal aorta is equal to the number of visceral arches, but the two anterior pairs, viz., those traversing the wall of the pharynx parallel with those parts of its supporting skeleton known as the mandibular and hyoidean visceral arches respectively (see p. 456), are found in adult forms only as remnants in connection with the carotid arteries. Whatever may have been the case in primitive forms, these first two arterial arches have now no part in aërating the blood, this function being performed by the succeeding pairs of arches, along whose course only are gill-sacs developed. We shall find that the arterial system near the heart is in all groups of Craniata a modification of the arterial arches just described.

The fore-limb is supplied by a vessel called the subclavian artery, but the origin of this differs in the several classes of the phylum. In Amphibia, Lizards and Mammalia other than Cetacea, it arises from the epibranchial artery near or behind the fourth visceral arch, while in Crocodiles, Turtles, Birds and Cetaceans its origin is from the ventral end of the fourth visceral arch. As in both Lizards and Cetaceans these two vessels exist side by side, but only one of them supplies the fore-limb, it is clear that the subclavian arteries are not homologous throughout the group.

Each chamber of the heart is separated from the one behind by valves, which are flaps of membrane free to move in one direction so as to open and admit blood from behind, but restrained by tendinous chords from being driven further back than so as just to meet when the chamber contracts, and thus prevent any backward movement of the blood. In the conus there may be several transverse rows of pocket valves. These valves as their name implies are loose pockets of membrane which are pressed flat against the wall of the conus during the forward movement of the blood, but which when the conus contracts become filled with blood and swollen out so as to meet one another and prevent the reflux of blood into the ventricle.

The development of the liver has exercised a profound influence on the afferent part of the blood system corresponding to the hinder part of the subintestinal vein of *Amphioxus*. The vast

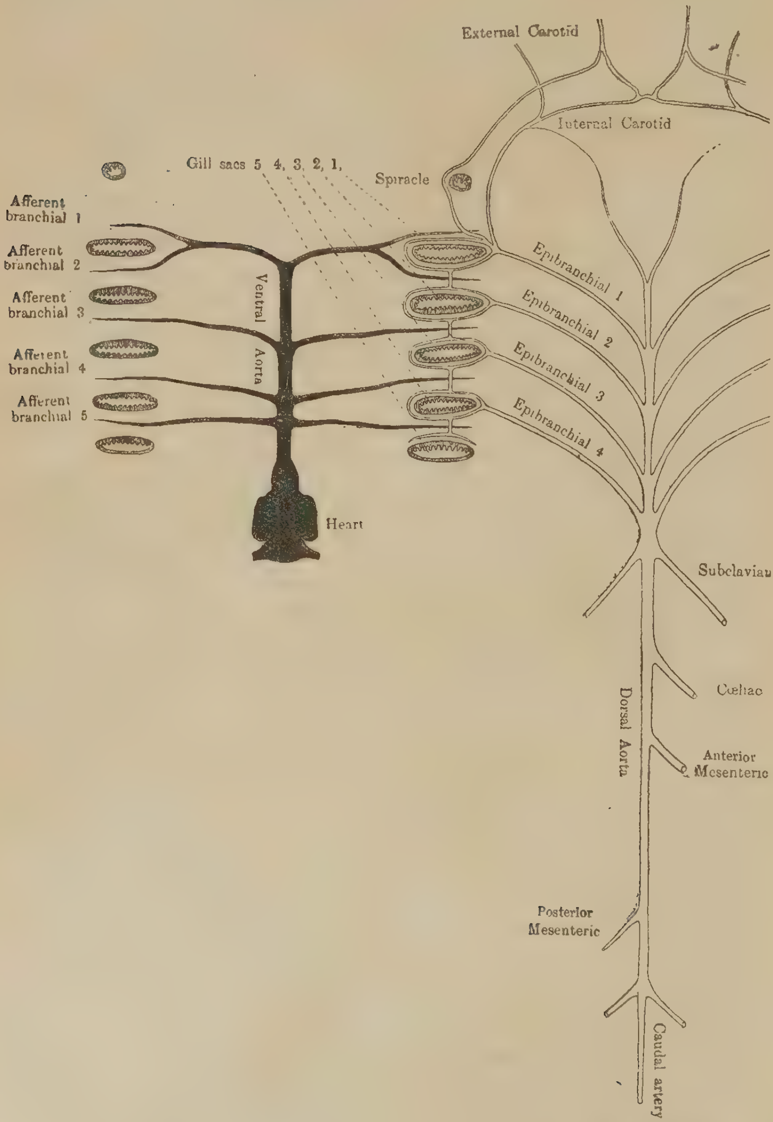


FIG. 213. Diagram of the ventral and dorsal aortas and their branches in *Scyllium* × about 1.

mass of liver-tubes projecting into this vein has broken it up into a network of capillary channels called the hepatic portal system. In front of this, where the vein enters the sinus venosus, it is known as the hepatic vein; behind, branches from the walls of the intestine so overshadow the original ventral trunk that this, embedded between the limbs of the spiral valve, appears as merely a small branch of the composite trunk or portal vein.

The blood from the muscles and kidneys, in a word, from the dorsal and outer parts of the coelom, collects into two longitudinal channels called the cardinal veins. These empty into the sinus venosus by transverse trunks called ductus Cuvieri. These transverse trunks divide the veins into anterior cardinals returning blood from the head, and posterior cardinals returning it from the rest of the body. In the tail the two posterior cardinals are represented by the median caudal vein, which further forward splits into two. Just as the course of the original sub-intestinal vein has been obstructed by the growth of the liver, so that of the posterior cardinal has been choked by the growth of the kidney tubes. The blood from the tail and hind limbs is forced to filter amongst these in a series of narrow channels called the renal-portal system. The part of the vein in front of the kidney retains the name posterior cardinal: the hinder part is called the renal-portal vein. A vessel running along the inner side of each kidney and collecting the blood which percolates through it from the renal-portal vein is termed the subcardinal vein. The vessels of the renal-portal system apparently do not give off capillaries to the kidney tubules; these latter receive all their blood supply from branches of the dorsal aorta.

The blood of Craniata has in addition to the ordinary amoebocytes a much larger number of oval or round cells impregnated with haemoglobin, called red blood-corpuscles. Haemoglobin has been mentioned when describing the earthworm *Lumbricus*, in which it is found diffused in the blood fluid. The great characteristic of haemoglobin is its power of forming a bright red, unstable compound with oxygen. This compound is formed in the respiratory organ and carried by the circulation to all parts of the body. In the capillaries it is broken up and the oxygen absorbed by the tissues. The haemoglobin having lost its oxygen changes in colour, and the impure blood which leaves the tissues is in consequence bluish. From the tissues the blood takes up carbon dioxide which, like the oxygen, is conveyed in loose chemical combination, though with the sodium of the blood instead of with the

haemoglobin. The carbon dioxide is set free in the respiratory organs.

On page 202 it was pointed out that both blood and connective tissue have been derived from a jelly-like secretion such as is found in Coelenterata. This in the embryo coelomate animal fills up the interstices between ectoderm, endoderm and coelomic sacs, these interstices being collectively termed the primary body-cavity or haemacoel. It was also pointed out there, that whereas in that part of the jelly which was converted into connective tissue a large number of fibres were developed, in the portion destined to form blood, on the contrary, no fibres appeared and the jelly remained fluid, and in consequence the amoebocytes which had wandered into it from the neighbouring epithelia were able freely to move about. In Annelida, Arthropoda and Mollusca certain of the blood-spaces acquire muscular walls derived from the adjacent coelomic sacs, and thereby attain contractility which may be specially localised in a dilatation called the heart. The spaces with muscular walls are the arteries. In Craniata a further differentiation has taken place: we find not only a definite heart and arteries leading away from it, but also equally definite veins leading into it as described above, and arteries and veins are connected with one another by narrow channels called capillaries with well-marked walls. Heart, arteries, veins and capillaries are all lined by a single layer of flattened cells called an endothelium, which has been developed from the flattening out and union of a certain number of amoebocytes. The capillaries possess no other wall, but arteries and veins have outside this a wall of elastic and fibrous connective tissue in which is embedded a zone of circular muscle-fibres. These structures are all derived from the adjacent coelomic sacs. The muscles of blood-vessels do not contract rhythmically and spontaneously like those of the heart, but are in a state of continued contraction called tone. This tone is under the control of the nervous system through the medium of special "vasomotor" fibres, and thus the supply of blood to an organ can be varied according to its need.

In Craniata however, outside the definite arteries, veins and capillaries, there exists a large portion of the haemocoel in the form of irregular channels and interstices, in many cases without definite walls, an endothelium being found only in the larger trunks. This system of spaces is known as the lymphatic system. It contains a clear fluid in which amoebocytes float, but no haemoglobin-containing cells, and at one or several points the main

trunks of the system open into the large veins. The finer branches of the system ramify amongst all the organs of the body. There is no circulatory current in the lymph canals except in those belonging to the viscera, but there are valves arranged so that when the lymph vessels are squeezed by the increase in diameter of neighbouring muscles when these contract, fluid can pass forwards in one direction but not backwards.

It will be seen that in Craniata, unlike Arthropoda and Mollusca, the blood, being everywhere confined to vessels with definite walls, does not directly bathe the tissues of any organ; but that materials must first diffuse through the walls of the blood-vessels into the lymph-spaces before they can reach the tissue. One explanation of the separation

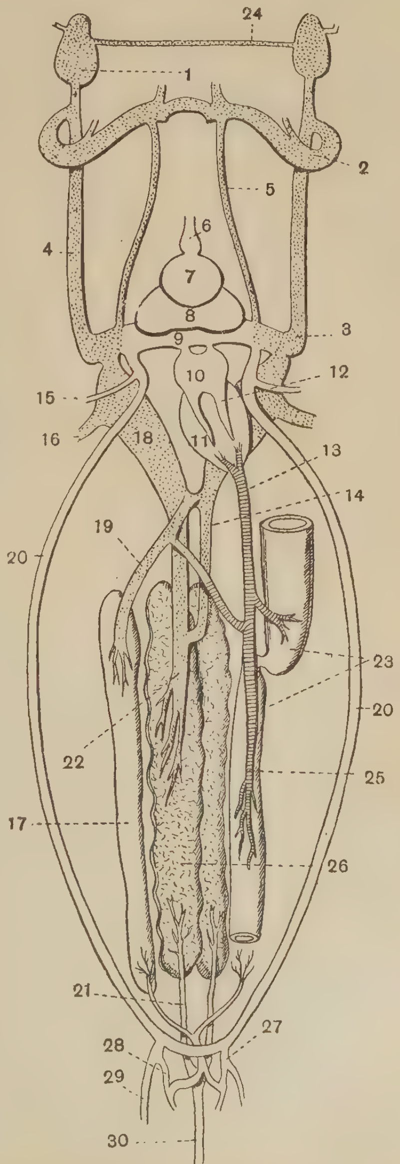


FIG. 214. Diagram of the venous system of *Mustelus antarcticus*. From T. J. Parker.

1. Orbital sinus. 2. Hyoidean vein. 3. Ductus Cuvieri. 4. Anterior cardinal vein. 5. Jugular vein. 6. Conus arteriosus. 7. Ventricle. 8. Atrium. 9. Sinus venosus. 10. Hepatic vein. 11. Liver. 12. Hepatic vein. 13. Hepatic portal vein. 14. Left cardinal vein. 15. Brachial vein. 16. Subclavian vein. 17. Gonad. 18. Posterior cardinal vein. 19. Spermatic vein. 20. Lateral vein. 21. Renal portal veins from caudal vein to kidney. 22. Right posterior cardinal vein. 23. Alimentary canal. 24. Vein connecting orbital sinuses. 25. Subintestinal vein. 26. Kidney. 27. Pelvic vein. 28. Cloacal vein. 29. Femoral vein. 30. Caudal vein.

of the lymph-system from the blood-system is that the haemoglobin is not diffused in the fluid of the blood, but is carried in cells which have no power of movement in themselves. Did these cells enter the lymph-system they would speedily block its finer channels.

The supply of amoebocytes to both blood and lymph is provided for by widely distributed actively growing nodules of cells which bud off amoebocytes into the adjacent lymph-channels. These packets of cells are called lymphatic glands: the largest collection

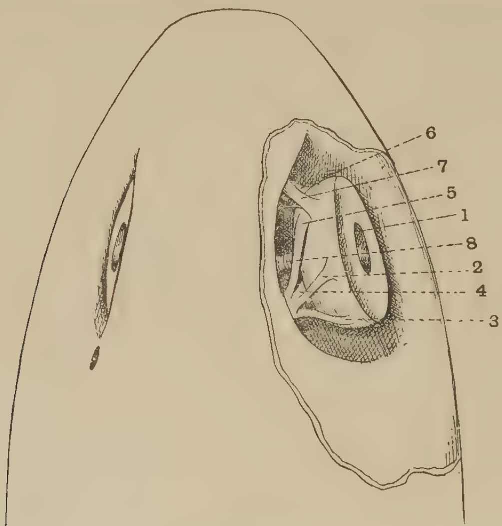


Fig. 215. Dorsal view of head of *Scyllium canicula* × 1. The right orbit has been exposed so as to show the muscles that move the eye and the second and fourth nerves.

1. Lens of the eye. 2. Superior rectus muscle of the eyeball. 3. External (or posterior) rectus muscle. 4. Inferior rectus muscle. 5. Internal (or anterior) rectus muscle. 6. Inferior oblique muscle. 7. Superior oblique muscle; the slender nerve entering this muscle is the fourth cranial. 8. Second cranial or optic nerve, the nerve of sight.

is in the spleen, an organ having several other functions, which is attached to the mesentery just dorsal to the posterior end of the stomach.

Coelom.

The muscles of the Craniata like those of the Cephalochorda are developed from the inner walls of a series of dorsal coelomic pockets, in a word, from myotomes. Unlike that of the Cephalochorda the trunk coelom does not become at first completely divided into separate sacs, the ventral portions of which fuse later. In the Craniata this stage is skipped in

development, and the coelom appears from the first as a pair of elongated sacs undivided below, but segmented above. After the complete separation of the dorsal portions as myotomes, the ventral parts of the two sacs unite beneath the intestine, whilst above it their walls become apposed, forming the vertical sheet of tissue known as the mesentery, in which the intestine is slung.

It is necessary of course for the efficient action of the eyes that they should be movable, and this is brought about by the space around the eyeball becoming converted into a cavity called the orbit, which in the lower Craniata is continuous with the anterior cardinal vein, and thus contains blood (Figs. 214 and 215), but which in the higher Craniata is a lymph space. To each eyeball six muscles are attached, two arising from the anterior part of the orbit and inserted one above and one below the eyeball, and named respectively the superior and inferior oblique; and four arising close together from the posterior corner of the orbit and inserted on the eyeball, one above and one below, the superior and inferior recti, and one antero-laterally, the internal or anterior rectus, and one postero-laterally, the external or posterior rectus.

The proboscis cavity and collar cavities of the Hemichorda are represented in the Craniata by two pairs of cavities found in the embryo, in advance of all the myotomes, termed the head-cavities. The anterior of these, termed the pre-mandibular, is joined to its fellow by a very narrow canal running underneath the eyes—the pair really constitute a bilobed cavity—from whose walls the inferior oblique, superior, inferior and internal recti muscles are developed.

The collar-cavities are represented by the mandibular cavities, a pair of long, narrow cavities running down the sides of the mouth, joining the splanchnocoel behind and curving up over the eye on each side. From the wall of the dorsal portion of the cavity the superior oblique muscle is derived. The external rectus muscle arises from the first myotome. The muscles derived from the anterior head-cavity are supplied by a common nerve, the third cranial; the superior oblique is supplied by the fourth, and the external rectus by the sixth cranial.

Most of the muscles which compress or expand the gill-sacs are derivatives of the wall of the unsegmented ventral portion of the coelom. From the inner wall of this part of the coelom all the muscles of the alimentary canal arise; these in Craniata are longitudinal as well as circular, and the muscles in the walls of the blood-vessels also arise from the coelomic wall. From the myotomes are

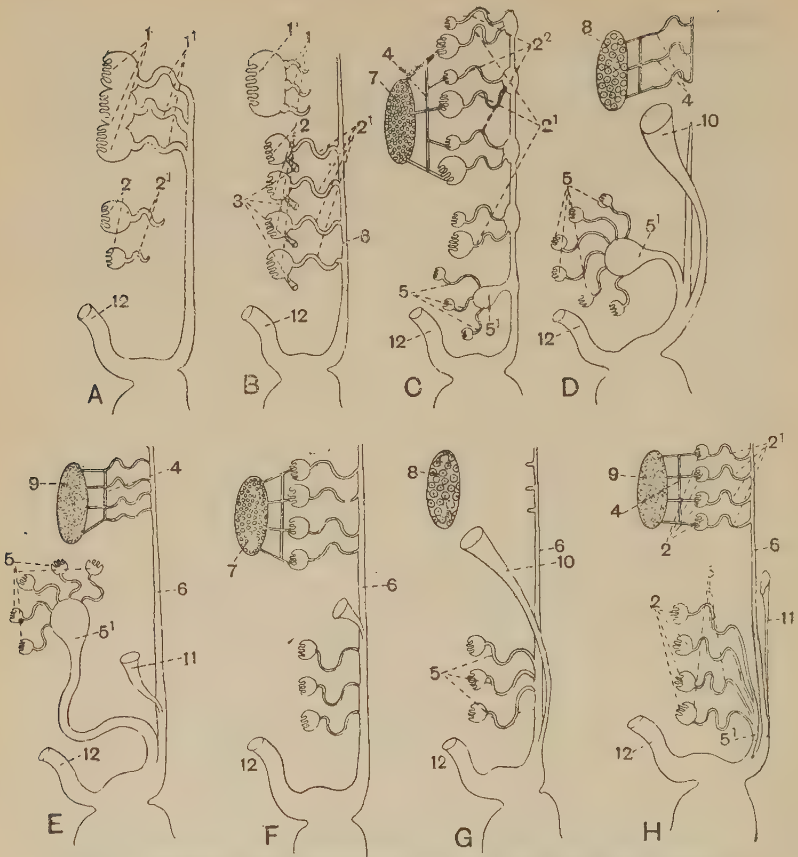


FIG. 216. Illustrating the development of the excretory and reproductive systems in Craniata.

A. The pronephros in functional activity, the mesonephric tubules being formed. B. The pronephros degenerating, the mesonephros in functional activity. C. The mesonephros connected with the genital organs by vasa efferentia in its anterior portion, the pelvis of the metanephros and the metanephric tubules being formed. D, E, represent the condition which is found in the higher Craniata. D. The condition in the female. The mesonephros connected with the ovary by vasa efferentia and in process of degeneration disconnected from the mesonephric duct. The metanephros fully formed and also the oviduct. E. The condition in the male. The capsules of the mesonephros have disappeared. The metanephros is fully developed, the oviduct is vestigial. F. The condition in the embryo Elasmobranch. The mesonephros is connected by vasa efferentia to the genital organ. The oviduct is arising by a splitting of the longitudinal duct. G. The condition in the female Elasmobranch, the hinder portion of the mesonephric duct alone persists and receives the metanephric tubules. The oviduct is separated from the longitudinal kidney duct. H. The condition in the male Elasmobranch. The mesonephros is connected with the testes, the oviduct is vestigial.

1. The pronephric chamber produced by the fusion of several nephrotomes. 1[1]. The pronephric tubules. 2. The Malpighian capsules of the mesonephros. 2[1]. The primary mesonephric tubules. 2[2]. The secondary mesonephric tubules. 3. The peritoneal funnels of the mesonephros. 4. The vasa efferentia and the longitudinal duct which unites them. 5. The Malpighian capsules of the metanephros. 5[1]. The ureter. 6. The archinephric duct. 7. Young genital organ. 8. Ovary. 9. Testes. 10. Oviduct. 11. Vestigial oviduct in male. 12. Rectum.

derived the muscles by which the locomotion of the animal as a whole is carried out. In the lower Craniata these have the same simple arrangement as was found in the case of *Amphioxus*, but in the higher forms where the movements are complicated by the development of limbs, these muscles are divided into numerous bundles with a very complex arrangement. All the muscles derived from the myotomes are composed of striated fibres. Most of those governing the movements of the alimentary canal and blood-vessels are composed of smooth fibres, but to this statement the muscles of the heart form an exception. These latter, the cardiac muscles as they are named, are cross-striated, but they are nevertheless very different from the cross-striated muscles derived from the myotomes. The cardiac muscles are short, thick fibres clearly divided by transverse septa into the cells to which they owe their origin. Each cell has a single nucleus. Neighbouring fibres are connected together by cytoplasmic bridges so that they contract together. Muscles derived from the myotomes consist of long fibres, each the product of a single cell but each containing numerous nuclei. These nuclei are scattered throughout the substance of the fibre, each embedded in a little islet of unmodified cytoplasm.

Urino-genital organs.

The excretory and reproductive organs are closely related in development, and by recent research their relation to those of the Cephalochorda has been made tolerably plain. The unit in the excretory system is a tube opening into the body-cavity at one end and at the other into a longitudinal duct which opens into the proctodaeum behind. The section of the body-cavity into which it opens is termed the nephrotome. The nephrotome is really a portion of the segmented division of the body-cavity lying immediately beneath the myotome into which at first it opens; it is also connected with the splanchnocoel below.

The kidney tube is in fact an outgrowth of the nephrotome; the longitudinal duct, which is termed the archinephric duct seems

to be made up by the fusion of the outer portion of successive kidney tubules. The kidney in Vertebrates is usually said to be divided into an anterior, a middle and a posterior region termed pronephros, mesonephros, and metanephros respectively, but these three portions are of very different values. The pronephros consists of two or three, rarely five or six tubules, which are outgrowths from nephrotomes which lie immediately below the region of the gills—for which reason the pronephros is sometimes termed the head-kidney. In each nephrotome there is formed a protrusion from its inner wall which abuts on the dorsal aorta. The protrusion takes the form of a plug containing a plexus of blood-vessels projecting into the cavity of the nephrotome. From this cavity the blood is only separated by a thin layer of epithelium, so that water can pass by diffusion from the blood into the nephrotome. This plug is termed the glomerulus. These anterior nephrotomes fuse with one another so as to form one cavity on each side—and this cavity, the so-called "pronephric chamber," sometimes becomes completely shut off from the splanchnocoel (as in Fish), sometimes (as in Amphibia) its opening into the splanchnocoel enlarges so that it ceases to be distinguishable from the latter space. The pronephros only persists during the early larval condition of the animal. As the animal grows it entirely disappears. It is to be looked on as a precocious development of the most anterior tubules of the kidney to serve the needs of larval life.

The middle portion of the kidney is called the mesonephros. In this region the nephrotomes remain separated from one another and constitute what are known as the Malpighian capsules of the kidney, and into each of these capsules a glomerular plug projects. In the lower Craniata (Elasmobranch, Fishes, Amphibia) the nephrotomes retain their connection with the splanchnocoel by long necks which become ciliated and are known as ciliated peritoneal funnels, but in all the higher Craniata the nephrotomes become definitely shut off from the splanchnocoel. The nephrotome or Malpighian capsule can bud off a similar smaller capsule which in turn produces a kidney tubule, the so-called secondary tubule. The tubule produced by the original nephrotome is called the primary tubule. The secondary tubule opens into the longitudinal duct which becomes enlarged so as to receive primary and secondary tubules. The longitudinal duct thus becomes somewhat moniliform, *i.e.* with alternate swollen and narrow places (C, Fig. 216). In the hinder region of the kidney or

metanephros there is essentially the same structure as in the mesonephros, but not only primary and secondary but tertiary tubules are produced, and all these tubules open into a single enlargement of the archinephric duct, which is termed the pelvis of the kidney. This pelvis tends to be separated by a constriction from the rest of the archinephric duct, and the neck of the communication between the two constitutes the ureter, and as the animal grows in length the ureter is drawn out into a long tube. (E, Fig. 216).

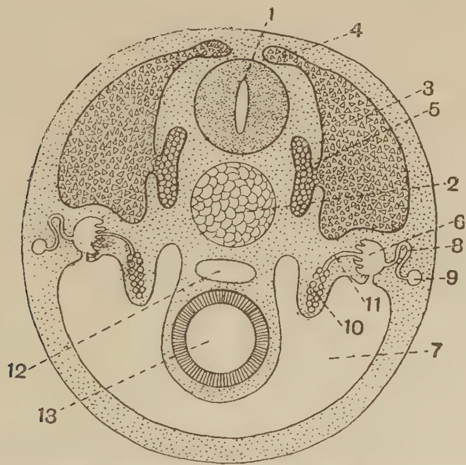


FIG. 217. Diagrammatic transverse section of an Elasmobranch embryo in order to show the development of renal and genital organs.

1. Nerve-cord. 2. Notochord. 3. Myotome. 4. Dorsal sclerotome. 5. Ventral sclerotome. 6. Nephrotome. 7. Splanchnocoel. 8. Mesonephric tubule. 9. Archinephric duct. 10. Rudiment of genital organ. 11. Vas efferens. 12. Dorsal aorta. 13. Alimentary canal.

The mesonephros, or rather some of its primary tubules, enter into close connection with the genital organ. The genital cells in Craniata at their first appearance seem to consist of groups of cells segmentally arranged, and these cells originate from the inner wall of the splanchnocoel just below the point where it communicates with the nephrotome. As they increase in number and bulk the segmental arrangement is obliterated, but from each originally separate mass of cells strings of cells originate which grow inwards into the connective tissue above the splanchnocoel and constitute the genital tubes. These genital tubes meet and connect up with

a series of tubular outgrowths from some of the primary nephrotomes of the mesonephros, which constitute what are called the vasa efferentia.

In the male the genital tubes persist throughout life and form the seminal tubes which make up the testes, and the ripe spermatozoa find their way out through the vasa efferentia, the mesonephric tubules and the archinephric duct, and this latter thus constitutes a vas deferens. In the female the vasa efferentia disappear, the genital tubes termed egg-tubes remain solid and their terminal cells enlarge and form ova, which are thus left isolated in the centre of a mass of connective tissue called the ovarian stroma. At the period of ripeness these eggs swell so much as to burst through this stroma into the splanchnocoel, whence they escape by pores situated near the anus (Eels and Lampreys) or by tubes, the oviducts opening in the same position, which seem to have been developed from grooves in the roof of the splanchnocoel leading to the pores. The oviducts of Elasmobranchii are peculiar in that they seem to be formed by a splitting of the archinephric duct (F, G, H, Fig. 216).

The mesonephros is thus distinguished from the metanephros by being the sexual region of the kidney. In most cases it persists throughout life only in the male, vestiges only being found in the female, but in some primitive types of fish, such as the Sturgeon and in Amphibia, mesonephros and metanephros are not clearly differentiated from one another, and a fully developed metanephros with pelvis and ureter is only found in Reptiles, Birds and Mammals.

If the above description has been followed it will be evident that the nephrotomes of Craniata correspond closely in position and origin to the gonadic pouches or gonocoeles of *Amphioxus* and have nothing to do with the excretory organs of that animal.

They are in fact coelomiducts, and it appears probable that they originally served as outlets for the genital products and correspond to the pores which are formed in the walls of the gonocoeles of *Amphioxus* at the period of sexual maturity. They still function as outlets for the spermatozoa in most Craniata, and the reason why they have ceased to serve as passages for the eggs is probably to be found in the circumstance that the eggs of all Craniata have become swollen in size owing to the accumulation of yolk so that they are no longer able to pass through such narrow passages as the kidney tubules afford, and hence have to find their way out in another manner.

The excretory function of the kidney tubules on this view would not be their original one; it would be a secondary function which had gradually supplemented the primary one. It must be remembered that the function of the whole coelomic wall is excretory, and any convenient opening which allows its contents to escape may develop into an excretory tube. This change of function has almost certainly occurred in Polychaeta, Annelida and in Mollusca, as well as in Craniata. Since the archinephric duct opens into the terminal portion of the alimentary canal behind, the faeces (as the indigestible remnants of the food are termed), the true excreta and the genital cells are all expelled through the same opening, which on this account has received the name cloaca which the Romans bestowed on their common sewer.

Division I. Cyclostomata.

The Craniata are divided into two main groups, namely, the Cyclostomata and the Gnathostomata. The former division, distinguished by the absence of true visceral arches and of jaws, includes at the present day only a few, probably degenerate, worm-like animals, with short tails like *Amphioxus*, and with naked skins. The name Cyclostomata means Round-mouthed (Gk. κύκλος, a circle; στόμα, mouth), and alludes to the circumstance that the edges of the mouth are stiffened by a ring-shaped cartilage, the annular cartilage, so that the mouth cannot be closed (2, Fig. 220). There is a piston-shaped tongue supported by a lingual cartilage, and the whole is protruded by a muscle attached to the annular cartilage in the lips (Fig. 219). Both the tip of the tongue and the walls of the stomodaeum are beset with horny teeth, developed from the agglutinated cells of the skin. The expansion of the stomodaeum causes the mouth to act like a sucker, and the whole animal is thus enabled to adhere to some foreign body, such as a stone, or to some victim, usually a fish, in which case the rasp-like tongue works a hole in the flesh of the prey. The stomodaeum is greatly elongated and is supported in its roof by several broad cartilages, the so-called labial cartilages; in consequence the eyes and gill-slits appear to be pushed very far back.

Structure.

The condition of the sense-organs is one of the most marked characteristics of the Cyclostomata. The nose is represented by a single sac placed far back in consequence of the elongation of the

stomodaeum, as above explained. This single sac is drawn out into a long tube passing beneath the brain, and in one order, the Myxinidae or Hag-fishes, this opens into the roof of the stomodaeum. The tube-like prolongation is really the pituitary body, which in the embryo develops close to the nasal sac. The groove connecting the two organs becomes closed so as to form a canal, and then by the great development of the roof of the suctorial mouth the external openings of the two organs are widely removed from one another, although internally their cavities communicate with one another.

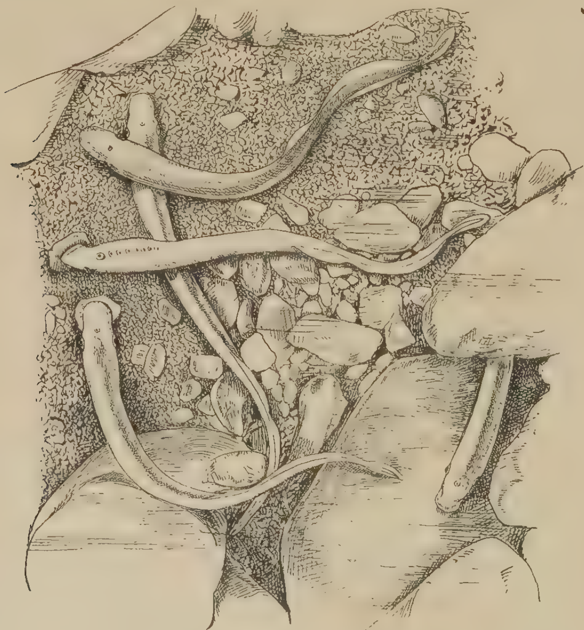


Fig. 218. The Musk Lamprey, *Petromyzon wilderi*, in the act of spawning. From Bashford Dean and Sumner.

The eye develops no proper cornea or aqueous humour, the lens remaining in connection with the skin. The ear is represented either by two semicircular canals and a vestibule (or sacculus) in the Lamprey, or by a single circular membranous tube in the Hag-fish which corresponds to the vestibule and one semicircular canal.

The gill-slits, usually seven in number, have the form of regular gill-sacs, recalling those of the Hemichorda, only without the

tongue-bars. The external opening is circular; the connection with the gullet, on the other hand, is a vertical slit (Fig. 219).

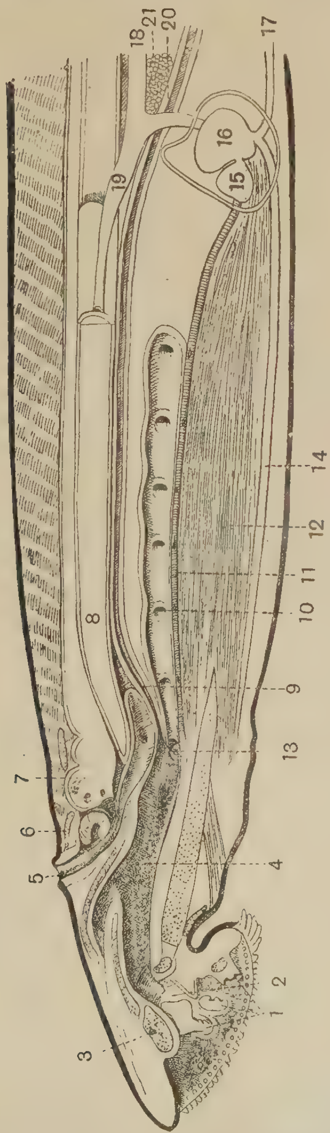


FIG. 219. The Lamprey, *Petromyzon marinus*; right half of a female specimen, the various structures being, for the most part, seen in longitudinal section (nat. size).

1. Horny teeth on inside of stomodaeum. 2. Mouth. 3. Dorsal half of annular cartilage in section. 4. Mouth cavity. 5. Nasal aperture. 6. Nasal capsule lying over nasal sac. 7. Brain. 8. Notochord. 9. Oesophagus. 10. Respiratory tube. 11. Ventral aorta. 12. Retractor of tongue. 13. Velum. 14. Inferior jugular vein. 15. Ventricle. 16. Auricle. 17. Hepatic vein. 18. Posterior cardinal vein. 19. Anterior cardinal vein. 20. Intestine. 21. Ovary.

The whole set of sacs is supported on a framework of cartilage which in its complete form as seen in the Lampreys, consists of

longitudinal dorsal and ventral bars, and connecting cross-pieces passing between the sacs which give off branches encircling their outer openings (Fig. 220). The whole of the branchial basket, as it is called, is a development of the dermis and has probably nothing to do with the visceral arches of the Craniata, as will be shown later. Since however bars corresponding to true visceral arches are found in Hemichorda and Cephalochorda, it is almost certain that their absence in Cyclostomata is a secondary phenomenon, and indeed, as we shall see immediately, remnants of true visceral arches are possibly represented by certain cartilages connected with the skull. The reason for their disappearance is a difference in the

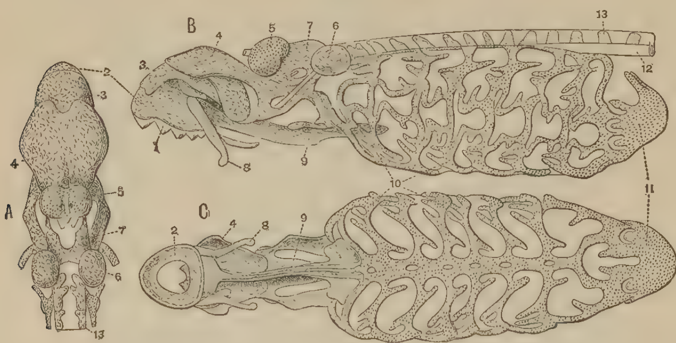


FIG. 220. A, dorsal, B, lateral, and C, ventral view of the skull of *Petromyzon marinus* × 1 (after Parker).

1. Horny teeth. 2. Annular cartilage. 3. Anterior labial cartilage. 4. Posterior labial cartilage. 5. Nasal capsule. 6. Auditory capsule. 7. Dorsal portion of trabeculae. 8. Lateral distal labial cartilage. 9. Lingual cartilage. 10. Branchial basket. 11. Cartilaginous cup supporting pericardium. 12. Sheath of notochord. 13. Anterior neural arches fused together.

method of expanding the branchial sacs from that which obtains in all other Craniata. For whereas in these latter the branchial sacs are expanded by the spreading out of the visceral arches like the ribs of an umbrella and are contracted when these arches fall together, in Cyclostomata each sac has its own radiating and circular muscles which enable it to contract and expand like a heart, and the rhythm can be reversed since water can and does enter as well as leave the gill-slits by the external pores when the animal has its mouth applied to a victim.

The commencement of the true alimentary canal is marked, as in *Amphioxus*, by a velum. What corresponds to the hyperpharyngeal groove in that animal is in many species of Cyclostomata

completely constricted off from the remainder of the gullet and is known as the oesophagus, though this word is used in a different sense from that in which it is used in the case of the Gnathostomata. The lower part of the gullet which communicates with the gill-slits in these cases ends blindly behind and is called the respiratory tube.

The hinder part of the alimentary canal is a nearly straight tube, the spiral valve having a very slight deviation from a straight course. There is no dilatation of any kind in its course. The large liver empties its secretion by the bile-duct, which opens into the intestine a short distance behind the branchial region.

The skull consists of the simplest elements, viz. the trabeculae, with a wide hole for the infundibulum, and the parachordals, which form only a slender arch over the hinder part of the brain, but develop also a low side wall throughout their extent with which the simple auditory capsule is fused. There is a loop of cartilage attached to each parachordal termed the subocular arch and a curved bar of cartilage behind this which is attached above to the skull and passes down along the pharynx. In Myxinoidea the latter encircles the pharynx and unites with its fellow in the mid-ventral line and joins the cartilage supporting the tongue. This second arch is termed the hyoid, and with some plausibility both it and the subocular bar are regarded as degenerate remains of the first two visceral arches of other Craniata. The nasal capsule is represented by cartilage stiffening the nasal tube. The brain is remarkable for having a thin membranous roof except just at the front end of the hind-brain where a narrow band of nervous matter represents the cerebellum.

The only fins present consist of a fringe of skin similar to that found in *Amphioxus* surrounding the hinder end of the body in the vertical plane. This fringe is divided by a notch into an anterior (or dorsal) and a caudal fin. The dorsal fin is supported by cartilaginous rays situated above which represent the neural arches which protect the spinal cord; the caudal fin has, in addition to these, rays situated below which are to be regarded as haemal arches. A caudal fin of this description, which the notochord divides into two equal lobes, is called diphycercal.

Besides the neural arches (13, Fig. 220) and small haemal arches in the tail no other cartilage is developed in connection with the axial skeleton, the notochord with its thick fibrous sheath persisting unchanged throughout life.

The pericardium is not completely separated from the remainder of the body-cavity, and the genital organs take the form in both sexes of a single median ridge projecting into the body-cavity (21, Fig. 219). No connection of the testis tubules with the kidney tubules exists, nor is there any trace of an oviduct, since both ova and spermatozoa are freely shed into the body-cavity and escape by two abdominal pores or simple openings in the body-wall placed ventrally to the openings of the kidneys. Inasmuch as these latter open directly to the exterior and are quite independent of the opening of the intestine, which is placed more ventrally, we may state that no cloaca has yet been developed.

Classification.

Living Cyclostomata, represented by a single class which may be called Marsipobranchii (Gr. μάρσιπος, a pouch), are divided into two orders: (i) PETROMYZONTIDA, (ii) MYXINOIDEA.

(i) In the first order, familiarly known as the Lampreys, the pituitary body appears as a blind process from the nasal sac: each gill-sac opens directly to the exterior, and the hyperpharyngeal groove is separated from the rest of the alimentary canal as a distinct tube, the so-called oesophagus.

The Lampreys (*Petromyzon*) are conspicuous in the early spring, when they ascend small brooks to spawn. Several species inhabit the rivers of Great Britain, Canada and the United States, but the differences between them are trifling, depending mainly on the development of the horny teeth covering the tongue. One species, *Petromyzon marinus*, attaining a much larger size than the others, inhabits the sea. It may reach a length of three feet, whereas the other forms do not grow longer than from ten to twelve inches. The eggs of Lampreys develop into a most interesting larval form which stands in many respects nearer to the other Craniates than does the adult and supplies an intermediate stage between *Amphioxus* and an ordinary Craniate. This larva is called the Ammocoetes, and its mode of life resembles on the whole that of *Amphioxus*. Like that animal the Ammocoetes lives on what is brought by the currents of water, produced by the cilia inside the velum. The thyroid gland, which, as we have seen, represents the endostyle, remains open, and still performs its primitive function of secreting a cord of mucus, which is carried up dorsally by a ciliated groove, the peripharyngeal band, situated just behind the velum. The hyperpharyngeal groove is represented by a dorsal strip of ciliated cells, the current produced by which sweeps the mucus

backward into the alimentary canal just as it does in *Amphioxus*.

The tubular suctorial stomodaeum is represented by a hood-like upper lip and a distinct short under lip, and when the mouth is contracted the velum is produced into tentacles just as in the Urochorda and in *Amphioxus*. The lateral eyes are exceedingly rudimentary, but there is a large pineal eye, and the nasal sac has a median septum.

(ii) The MYXINOIDEA are characterised by the persistent connection of the pituitary body with the stomodaeum, so that there is a tube leading from the nasal sac to the mouth. There are eight tentacles called barbels at the sides of the mouth, and there is no special oesophagus distinct from the rest of the gullet. The skin has a double series of mucous glands placed at the sides of the body, and so much mucus can be thrown out that a large amount of water can be rendered semi-solid. The intestine has no spiral valve. The Myxinoidea are the animals known as Hag-fish. They adhere to fish on whose flesh they feed, but, unlike the Lampreys, they can actually burrow into their victims so that the stomodaeal region is completely buried. In connection with these habits the stomodaeal region is enormously elongated, and the eyes remain in a rudimentary condition, whilst the gill openings are pushed very far back.

The Myxinoidea include two genera, *Bdellostoma* and *Myxine*. In the former, which is a genus inhabiting the southern Atlantic and Indian Oceans, the gill-sacs are seven in number on each side and open separately; in *Myxine*, on the other hand, each external opening of the six gill-sacs is drawn out into a long tube, and the tubes of each side curve back and unite to open by a common atrial pore placed so far back that the animal can insert almost half its length into the body of its victim without interfering with its breathing. The branchial basket is vestigial in this genus. The portal vein is rhythmically contractile, and thus constitutes an accessory heart for the purpose of forcing venous blood through the capillaries of the liver. *Myxine* is common on both the Atlantic and Pacific coasts of North America and on the European coast.

DIVISION II. GNATHOSTOMATA.

The great division of the Gnathostomata includes all the remaining Craniata, and is characterised by the development of definite visceral arches, jaws and paired limbs. The visceral arches

are jointed rods developed from the inner or splanchnic wall of the coelom; they cannot therefore be considered as corresponding to the branchial basket of Cyclostomata. They are placed in the forms which retain gill-slits between these openings, and hence are often called gill-bars. The first pair of visceral arches lie in the sides of the mouth, and consist on each side of two pieces, hinged on one another and called the upper and under jaws respectively. By the motion of these on one another the mouth can be opened and closed. The nose is always represented by two sacs and the ear has three semicircular canals.

The Gnathostomata are divided into five classes which can be grouped into two sub-divisions. In the first sub-division, termed Anamnia, which includes Pisces and Amphibia, the whole of the egg is converted into the body of the embryo, and though a ventral protrusion of the hind gut termed the allantois may be formed, this does not function as a special embryonic organ. In the second sub-division, termed Amniota, a portion of the egg is converted into a hood termed an amnion, which envelops the body of the embryo and is cast off at birth, and the allantois is enlarged during embryonic life and functions as respiratory or nutritive organ. The greater part of the allantois is cast off with the amnion at birth, and only the stump persists in the adult and functions as urinary bladder. In the first three of these the temperature of the body varies with that of the surrounding medium.

Sub-division I. Anamnia.

Class I. Pisces.

Gnathostomata with fins supported by fin-rays and breathing chiefly by gills.

Class II. Amphibia.

Gnathostomata with pentadactyle or five-fingered limbs and without fin-rays. Gills and gill-slits functional in the young but generally entirely lost in the adult. An allantois is formed which functions as a urinary bladder in the adult, but has no function in the embryo. The skin is soft and moist.

Sub-division II. Amniota.

Class III. Reptilia.

Gnathostomata with pentadactyle limbs. The young are born similar to the adult. The allantois is greatly enlarged in the

embryo and has the function of a respiratory organ. The skin develops horny scales.

Class IV. Aves.

Gnathostomata agreeing with Reptilia in most points, but having a constant temperature independent of that of the surrounding medium. The skin is provided with feathers instead of scales and the fore limb is used as a wing.

Class V. Mammalia.

Gnathostomata agreeing in many points with Reptilia, but clothed with hair instead of scales. The body, like that of Aves, has a constant temperature independent of that of the surrounding medium. The young are nourished after birth by the secretion of certain glands of the mother termed milk glands or mammary glands.

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CHAPTER XX

SUB-PHYLUM IV. CRANIATA

Division II. Gnathostomata.

Sub-division I. Anamnia

Class I. Pisces

The class Pisces, or true Fishes, are not, as many would imagine, characterised by their gills (since some Amphibia retain these throughout life), but by their fins. In addition to the vertical flap of skin with which we have become acquainted in the case of the Cephalochorda and the Cyclostomata, we find typically two pairs of lateral flaps, an anterior pair called the pectoral fins, and a posterior pair known as the pelvic fins (Figs. 224 and 225). Both from a study of their development and their condition in the oldest fishes, it is believed that the paired fins are derived from the division of two originally continuous lateral flaps, of which the intermediate portions have disappeared. It is possible even probable that the wall of the atrial cavity of *Amphioxus* is homologous with this lateral fold: if this be so we may argue that the absence of lateral fins in the Cyclostomata is a result of secondary degeneration since *Amphioxus* represents a much more primitive level in the evolution of the Vertebrate stem than Cyclostomata.

Characters

While the possession of paired fins discriminates Pisces from the lower Vertebrata, the forms of these members equally sharply mark Pisces off from the class with which they are most nearly allied, namely Amphibia. In all Pisces the limb or fin is a blade-like organ which never exhibits the slightest resemblance to the typical form familiar to all in the human limb, but Amphibia have as representatives of the paired fins limbs in which the plan of the human arm and leg can be at once recognised. The blade-like type of fin is known as the ichthyopterygium (ἰχθύς,

a fish; πτερύγιον, a little wing), the other type of limb as the cheiropterygium (χείρ, the hand). Pisces therefore are defined by the possession of ichthyopterygia.

The median and the paired fins are stretched on a skeleton with a two-fold origin, (i) a median series of cartilaginous or bony rods or pterygiophores which support the basal part of the fins, and (ii) a double series of horny fibres or bony dermal fin-rays which support the distal part of the fins. The horny fibres are termed ceratotrichia, the bony dermal rays lepidotrichia; both are from the modification of the superficial layer of the dermis which immediately underlies each side of the fin-blade.

Taking a broad view of the various types of fish living at the present time, we find that the old common-sense division of the group into Cartilaginous fish or Chondrichthyes and Bony Fish or Osteichthyes is endorsed by the latest scientific writers on the subject. Cartilaginous fish have no true bone; calcareous matter may be, and often is deposited in the cartilage which is then said to be calcified, but the characteristic structure of cartilage persists. They are further characterised by possessing a peculiar form of scale termed the placoid which is a hollow tooth-like structure. They never possess an outgrowth from the alimentary canal containing air termed an air-bladder, the nostril or opening to the nasal sac is undivided and the eggs are few and large and are fertilised internally and have already undergone a considerable portion of their development when laid. In many, perhaps in most, cases the egg shell is absorbed in the oviduct and the embryo derives nourishment from the secretions of the oviduct and grows to a relatively enormous size before being born. To give an instance:— the Canadian Spiny Dog-fish *Squalus acanthias* attains a length of three or four feet and its ripe embryo may be eighteen inches in length.

In Osteichthyes on the contrary the bone is always present and the cartilage of the skull is always replaced by it to a greater or less extent: an air bladder is developed as an outgrowth from the alimentary canal behind the gill region, the opening to the nasal sac is divided into two by a bridge of bone: placoid scales may be present and indeed usually are present in the region of the stomodaeum but they are underlain and connected together by calcifications of the dermis which constitute the real effective scales of the Osteichthyes. The eggs are always small and in the vast majority of cases are fertilised externally and pass through a long larval

development before attaining the adult condition. Even in the few aberrant cases where fertilisation is internal and where the young are produced viviparously these young are nevertheless very small compared to the size of the parents.

Sub-class I. Chondrichthyes.

The Chondrichthyes include all the creatures known as Sharks, Dog-fish and Rays whilst the Osteichthyes include all other fish. The placoid scale, the only form of skin defence developed in this sub-class is a little spikelet consisting of a substance called dentine coated with enamel. The spikelet covers a little cone-like projection of the dermis, and it is covered in turn by the epidermis or true ectoderm. Dentine is a hard substance produced by the calcification of the ground substance of the dermal connective tissue. It differs from bone in the fact that it includes no cells within it but from the cells of the connective tissue in the cavity which it surrounds and which is called the pulp-cavity, processes are given off which penetrate the dentine and give rise to canals called dentinal canals. The core of soft connective tissue is called the dentinal pulp.

The spike therefore may be described as a little wart of dermis calcified on the outside. It pushes the ectoderm before it, and it becomes encrusted with crystals of carbonate of lime forming the enamel layer (Fig. 221). These closely set crystals are secreted by the inner or basal ends of the ectoderm cells. One would naturally expect that structures like scales, which are closely arranged all over the body, would also invade the stomodaeum, which is merely a part of the skin. This we find to be the case, but here the scales are very greatly enlarged in size and changed in function; they are the well-known teeth which are used for the purpose of retaining and lacerating prey which has been seized. The spike of the tooth is usually flattened and blade-like, and provided with strongly serrated edges. Fusions of several teeth can occur. The teeth are developed in a deep fold of skin, part of the stomodaeum, situated just inside the lower jaw, and usually speaking only the outermost row are in use at one time, the skin working forward the next set as each row wears out.

The Chondrichthyes are divided into two orders, viz. the Elasmobranchii and the Holocephali. In the former group the visceral arches are all distinct from the cranium. The gills are borne on

the walls of gill-sacs, and there is no common gill-cover to protect the external openings of the gills; the anterior external margin of each gill-sac being produced into a slight flap which can close the opening when it is pressed down. The skin is well covered with placoid scales, and the teeth are not fused together. In the Holocephali on the contrary, the upper half of the first visceral arch which in Elasmobranchii forms the upper jaw is indistinguishably fused with the cranium. There is a common gill-cover, the operculum, developed as a flap of skin arising from the hyoid arch which can

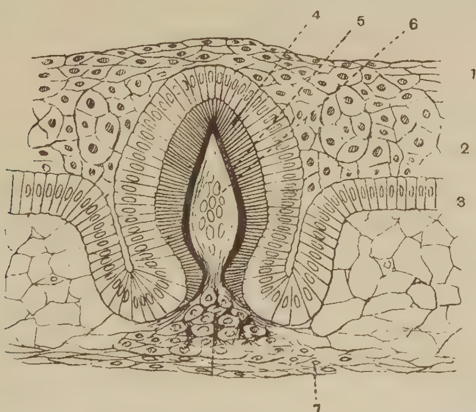

FIG. 221. Section through the skin of an Elasmobranch showing formation of a dermal spine. Highly magnified.

1. Horny layer of ectoderm. 2. Malpighian layer. 3. Columnar cells of ectoderm secreting 4. 4. Enamel. 5. Dentine (black). 6. Dentinal pulp. 7. Connective tissue.

cover all the gill-slits, and the septa dividing the gill-slits from each other are reduced in breadth, the gill-folds arising from the walls of the gill-sacs project slightly beyond the outer edges of the septa. The teeth are fused together to form great dentinal ridges with specially hard parts called tritors and the skin is naked, placoid scales being only developed on a peculiar tentacle which the male has developed on his head and which he uses to seize the female during copulation.

Order I. **Elasmobranchii.**

The Elasmobranchii includes the vast majority of fish classed as Chondrichthyes, and we shall therefore describe the structure of a typical Elasmobranch in order to give an idea of the organisation of Chondrichthyd fish. In a typical Elasmobranch the skull is much

better developed than in Cyclostomata. In the cranium the parachordals and trabeculae are firmly fused together so as to form a continuous plate and the pituitary fossa is reduced to a minute hole; there is a high and well-developed side wall and the roof extends a long distance forward. The sense-capsules, nasal and auditory, are well developed and firmly united with the cranium. The eyes are large and highly developed, and the side wall of the cranium is indented to make room for the spacious orbits in which the eyes move. There is a considerable part of the head in front of the brain, which usually also projects in front of the mouth. This is the rostrum or snout, and it is supported by three cartilaginous rods, one ventral and two dorsal, projecting from the front end of the cranium. These rods are the forerunners of the ethmoidal region in other forms. In many species the opening of the nasal sac is connected with the mouth by a groove called the oronasal groove (Fig. 226). There are usually six gill-clefts and seven visceral arches in Elasmobranchs. The first cleft, sometimes called the spiracle, is rudimentary and in some cases entirely absent. On the other hand there is one family, the Notidanidae, with two extra clefts behind, so that there are in all eight clefts and nine visceral arches in this family.

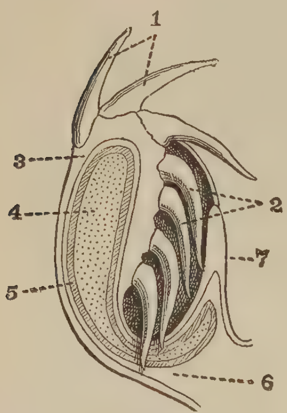

Fig. 222. Diagram of a section through the jaw of a Shark, *Odontaspis americanus*, showing the succession of teeth. From Reynolds.

1. Teeth in use. 2. Teeth in reserve. 3. Skin. 4. Cartilage of the jaw. 5. Encrusting calcification of cartilage. 6. Connective tissue. 7. Ectoderm lining the mouth.

The first pair of visceral arches form as we have seen the jaws. The upper jaw is known as the palatopterygoquadrate bar, a compound appellation derived from the names of the bones by which it is represented in the higher forms: the term is sometimes shortened to pterygoquadrate. The lower jaw is called Meckel's cartilage or mandibular bar: in front a strong ligament, the so-called ethmopalatine ligament, attaches the upper jaw to the skull. The second pair of arches are spoken of as the hyoid, and this too is divided into two portions, an upper, the hyomandibular, which is firmly connected to the cranium just below the auditory capsule, and a lower, the ceratohyal (Fig. 223). The upper jaw is

connected with the cranium either directly, by articulation with the cranium in front of the auditory region, an arrangement called autostylic and prevailing among recent Elasmobranchs only in the Notidanidae; or else the upper jaw has lost its articulating process with the cranium and is instead firmly connected or slung by ligament into the hyomandibular, which thus suspends the jaw from the skull. This arrangement, called hyostylic, is that seen in the majority of Elasmobranchs. A modification, termed amphistylic, occurs in Heterodontidae, where the jaw is slung by the hyomandibular but also has acquired direct articulation with the skull in front of the orbit. The remaining visceral arches have only

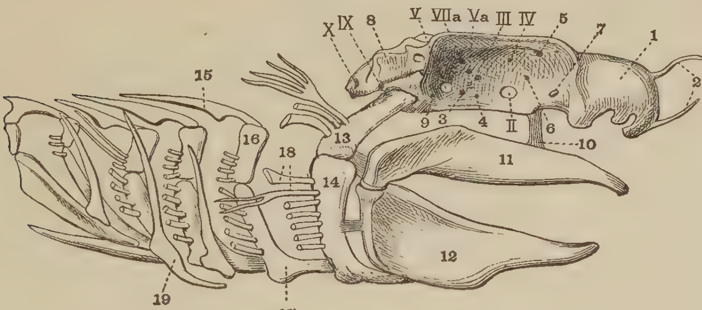

Fig. 223. Lateral view of the skull of a Dog-fish (*Scyllium canicula*) × ⅘. From Reynolds.

1. Nasal capsule. 2. Rostrum. 3. Interorbital canal for the passage of a blood-vessel. 4. Foramen for hyoidean artery. 5. Foramen for the exit of the ophthalmic branches of Vth and VIIth nerves. 6. Foramen through which the external carotid leaves the orbit. 7. Orbitonasal foramen which allows a blood-vessel to reach the nose. 8. Auditory capsule. 9. Foramen through which the external carotid enters the orbit. 10. Ethmopalatine ligament. 11. Palatopterygoquadrate bar. 12. Meckel's cartilage. 13. Hyomandibular. 14. Ceratohyal. 15. Pharyngobranchial. 16. Epibranchial. 17. Ceratobranchial. 18. Gill-rays; nearly all have been cut off short for the sake of clearness. 19. Extrabranchial. II, III, IV, V, Va, VIIa, IX, X. Foramina for cranial nerves.

a muscular connection with the skull and are termed the branchial arches, since to their sides are attached the gills. The branchial arches are jointed into several pieces, which are placed in an oblique position and so arranged that when they are raised by the levatores arcuum—muscles attaching them to the skull—they diverge and expand the gill-sacs lying between them. The segments of each branchial arch are typically four in number, named respectively pharyngobranchial, epibranchial, ceratobranchial, and hypobranchial. The first-named are situated in the dorsal wall

of the pharynx and are horizontal in direction ; the epi- and ceratobranchial stiffen the sides of the pharynx—the ceratobranchial being the main portion of the arch, whilst the hypobranchial pieces are found in the ventral wall of the pharynx and converge to unite in a median plate, the basibranchial. To the ceratobranchials are attached a number of thin rods of cartilage which run outwards in the wall of the gill-sac and are called gill-rays. Lying outside the visceral arches are a varying number of cartilaginous rods. Those situated at the sides of the gape are called labial cartilages, those external to the hinder visceral arches extrabranchials (19, Fig. 223). They are equivalent to gill-rays which have become detached from the arches.

The first gill-slit, called the spiracle, is situated between the jaw and the hyoid just outside the internal ear (Fig. 227). It is a narrow tube, and its use in the more typical forms appears to be to allow vibrations to come more closely in contact with the ear, and to admit the water for breathing. It is often entirely suppressed. The other slits are really flattened sacs, the walls of which are supported by the gill-rays and are raised up into thin folds richly supplied with blood-vessels, which are the true gills. A rudimentary gill, the pseudobranch, is sometimes developed on the front wall of the spiracle. No gill is developed on the posterior wall of the last gill-sac.

Vertebral column.

In Elasmobranchs we find, as in Cyclostomata, well-developed dorsal (or neural) and ventral (or haemal) arches, with their ends deeply embedded in the thick sheath of the notochord. This sheath consists partly of the primary sheath secreted by the notochordal cells which has been converted into cartilage by amoebocytes wandering into it and partly of a secondary sheath derived from the sclerotome (*v.* page 414), and it is divided into separate pieces called centra. Between the centra the sheath remains membranous, and in the middle of each centrum the notochord becomes very much narrowed, so that instead of being a uniform rod it is like a row of beads. The haemal arches meet beneath in the tail, but further forward they stretch out horizontally and become jointed ; their outer segments are the ribs, and this is the first appearance of these organs. The ribs project at the level of the centre of the fleshy masses formed by the myotomes. The inner segments of these arches are termed basiventrals. The ribs do not correspond to the outgrowths of the basiventrals in the tail because in one genus of the Osteichthyes (*Polypterus*) we find two sets of ribs on each side of the vertebral column one above the

other: the upper set correspond to the ribs of Elasmobranchs, the lower to the ribs of other fish and to the haemal arches of Elasmobranchs. There are usually twice as many neural arches as there are centra, and every alternate one is small and does not meet its fellow, and hence is called an intercalary piece: the haemal arches are generally as numerous as the centra but occasionally there may be ventral intercalary pieces. The cranium, visceral arches and centra are all strengthened by a calcareous deposit in the ground substance of the cartilage. This calcified cartilage

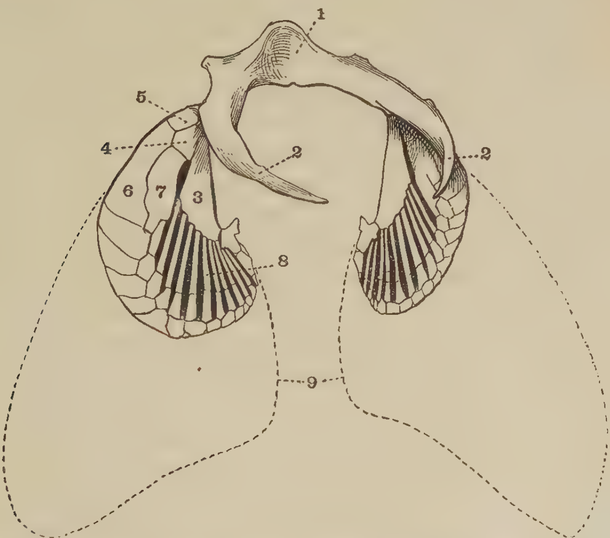

Fig. 224. Dorsolateral view of the pectoral girdle and fins of a Dog-fish, *Scyllium canicula*, $\times\frac{2}{3}$ From Reynolds. The gaps between the radialia are blackened.

1. Hollow in the midventral part of the pectoral girdle which supports the pericardium. 2. Dorsal (scapular portion) of pectoral girdle. 3. Metapterygium. 4. Mesopterygium. 5. Propterygium. 6. Propterygial radial. 7. Mesopterygial radial. 8. Metapterygial radial. 9. Outline of the distal part of the fin which is supported by horny fin-rays.

is to be carefully distinguished from true bone, which is entirely absent in Elasmobranchs.

The primitive tail fin of Vertebrata, as we have seen, is a fringe surrounding the end of the tail. Only a small and narrow remnant of this persists in Elasmobranchs, the whip-like end of the tail being bent up; beneath it there is a well-marked fin, and this together with the remains of the primitive caudal fin constitute a secondary

tail-fin, which is now denominated heterocercal, since the axial skeleton does not divide it into two equal parts (Fig. 227).

Limbs.

The paired fins are attached to hoops of cartilage (the limb arches), called respectively the pectoral and pelvic girdles, the pectoral being situated just behind the last gill-cleft, the pelvic just in front of the anus. The pectoral girdle extends a considerable distance up the side of the animal: the pelvic is little more than a transverse bar. The fins in modern Elasmobranchs are of what is called the uniseriate type, that is to say, there is a thick jointed main axis with cartilaginous rays attached only to its anterior border. Fossil Elasmobranchs show in one case, *Pleuracanthus*, a biseriate fin with rays attached to both borders; and in another, *Cladoselache*, a still more primitive condition, where the fin is merely a lateral flap supported by parallel bars of cartilage. By the coalescence of these at the base the axis was formed, and later by the disappearance of the rays on one side, the uniseriate fin. In *Cladoselache* there seems to have been no limb girdle. This is a newer development and must be regarded as a strengthening of connective tissue at the base of the fin in order to provide a firm insertion for the muscles moving the fin.

In the pectoral fin the basal portions of some of the rays coalesce to form two large cartilages called propterygium and mesopterygium, whilst the axis itself is called the metapterygium. In the pelvic fin of the male the axis bears distally a grooved rod which is termed the clasper, and is used in transferring spermatozoa to the female. The axis is called the basipterygium. The distal joints of the rays in both pectoral and pelvic fins are made up of numerous small cartilages called radialia.

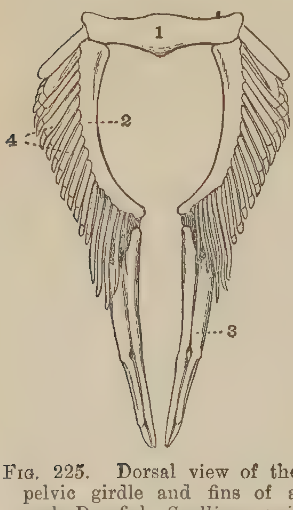

FIG. 225. Dorsal view of the pelvic girdle and fins of a male Dog-fish, *Scyllium canicula*. From Reynolds.

1. Pelvic girdle. 2. Basipterygium. 3. Clasper. 4. Radialia.

Brain.

The brain of Elasmobranchs is remarkable for the great development of the olfactory lobes, which are in close contact with the nasal sac and are attached by a narrow stalk to the cerebrum. This is only imperfectly divided into

two hemispheres and has nervous tissue on its roof as well as its floor. The cerebellum is developed into a great flap which projects back and covers the thin roof of the medulla oblongata (Fig. 207). It has also lateral outgrowths called cerebellar lobes.

Alimentary Canal.

The alimentary canal is considerably longer than the body and is consequently folded. It has, as a matter of fact, a U-shape: the first limb and a part of the next constitute the stomach, which is marked off from the intestine by a constriction and a powerful development of the circular muscles forming a sphincter or circular muscle. To the posterior aspect of the loop is attached the prominent spleen. The intestine, although outwardly straight, is probably derived from a corkscrew coil by the adhesion of successive turns: for the "spiral valve" which, as we said, is merely a ventral infolding, has a very strongly marked spiral course. The liver opens by the bile-duct into the beginning of the intestine, and close to its opening is situated that of the duct of the pancreas. A small gland of unknown function, the rectal gland, opens into the hinder end of the intestine.

The pericardium is almost completely separated from the rest of the coelom, communicating only by two narrow holes with it. The heart has the typical structure described in the last chapter (see p. 430). In the conus there are at least two transverse rows of pocket-valves, occasionally more. The arterial arches arising from the ventral aorta run up between successive gill-sacs and break up into capillaries on the surface of the gills: from these the blood is collected by vessels in the form of loops completely surrounding the gill-sacs. From these loops four pairs of epibranchial vessels arise and run backwards in the dorsal wall of the pharynx converging to form the single dorsal aorta, which supplies blood to all the hinder part of the body. The last gill-sac has a gill only on its anterior border; the blood from this does not reach the dorsal aorta directly but is connected by a transverse vessel with the loop surrounding the preceding gill-sac. The dorsal aorta gives off on each side a subclavian artery to the pectoral fin and then four median arteries which run down through the mesentery and supply the alimentary canal. These are named the coeliac, anterior mesenteric, lienogastric and posterior mesenteric arteries respectively (Fig. 227). The most anterior, the coeliac, has two important branches, (1) one supplying the liver and the proximal part of the stomach with arterial blood, and (2) the other supplying the anterior part of the intestine and the pancreas. The anterior

mesenteric artery supplies the greater part of the intestine and sends branches to the reproductive organs. The lieno-gastric supplies the posterior part of the stomach, the spleen and part of the pancreas. The posterior mesenteric supplies the rectal gland. After giving branches to the genital organs, kidneys and pelvic fins, the aorta continues its course into the tail as the caudal artery. From the two most anterior branchial loops a pair of vessels arise running forward in the dorsal wall of the pharynx and at the same time converging. These are the common carotid arteries, which supply blood to the head. Each divides into two main branches, an external carotid, which pierces the floor of the orbit and supplies the eye and the jaw, and an internal carotid, which pierces the floor of the skull near the middle line and supplies the brain. The pseudobranch on the front wall of the spiracle receives its blood from the hyoidean artery which, branching from the loop surrounding the first gill-sac, runs forward in the roof of the mouth parallel with the common carotid artery and eventually joins the internal carotid. In the venous system the anterior portion of the subintestinal vein is represented by a pair of hepatic veins returning the blood from the liver, opening into the sinus venosus close to the middle line, whilst the posterior portion has dwindled to a small vein embedded between the folds of the spiral valve; this however is joined by branches from the sides of the intestinal wall to form the main trunk of the portal vein. Both anterior and posterior cardinal veins are represented by wide, somewhat irregular spaces. Each anterior cardinal has an expansion called the orbital sinus which surrounds the eye. The two orbital sinuses communicate by an interorbital canal tunnelled in the base of the skull. The blood from the ventral sides of the gill-sacs and pharynx is returned to the ductus Cuvieri by a pair of independent trunks called the jugular veins. These are each connected with the anterior cardinal vein of its side by the hyoidean vein lying in a groove on the hyomandibular cartilage (Fig. 213). The blood from the tail is returned by a median caudal vein lying beneath the caudal artery and like it enclosed between the centra and the united ventral ends of the haemal arches. At the level of the posterior end of the kidneys the caudal vein divides into the two renal portal veins lying on the outer edges of the kidneys. These veins, as has been already explained (see p. 433), are the hinder portions of the posterior cardinal veins which break up into the renal portal system of capillaries. These filter amongst the kidney tubules and reunite

on the inner side of the kidney to form the spacious posterior cardinal sinuses, as the front portions of the posterior cardinals are named. These two sinuses lying ventrally to the kidneys partly coalesce. Each sinus curves forwards and outwards to join the ductus Cuvieri and at this point it is met by the so-called subclavian vein which returns blood from the region of the shoulder[1]. The pelvic vein receives the blood from the side of the cloaca by the cloacal vein and the blood from the pelvic fin by the femoral vein. It then opens into a longitudinal trunk, called the lateral vein, which runs along the side of the body beneath but parallel to the posterior cardinal vein. The lateral vein in front receives the brachial vein from the ventral side of the pectoral fin (not to be confounded with the subclavian from the dorsal region of the pectoral girdle) and then opens into the ductus Cuvieri. The cloacal veins further give off median branches which unite and then distribute blood to the viscera, so that some blood from the pelvic fin may also return to the heart through a portal system.

The ovary is a single ridge of the dorsal coelomic wall, its fellow which is indicated in the embryo having dwindled and disappeared; the oviducts are long and united far in front so as to open by a common internal opening, situated ventral to the liver (Fig. 226). In the middle of its length each oviduct has an enlargement caused by a thickening of its walls due to the development of gland cells. This is called the oviducal gland, and its function is to secrete the pillow-shaped elastic egg-shell. The egg is large and well charged with yolk. The oviducts unite posteriorly to open into the proctodaeum or cloaca behind the anus. There are two large testes, and these are united anteriorly and connected to the front end of each of the kidneys, which extend along the entire length of the abdominal coelom. The anterior region of the kidney or mesonephros (for no pronephros is developed) is narrow and its excretory function has almost disappeared. The testis is connected with the front end of the mesonephros by vasa efferentia. These vasa efferentia eventually open into a single coiled duct. This duct is the archinephric duct which has also lost its original function and become a vas deferens; it lies on the ventral surface of the kidney and conveys spermatozoa from the mesonephros to the cloaca. It enlarges at its hinder end into a vesicula seminalis. The posterior and functional part of the

[1] This vein has been described as receiving blood from the pectoral fin, but O'Donoghue has shown that this is a mistake, and that its blood is derived solely from the region of the shoulder.

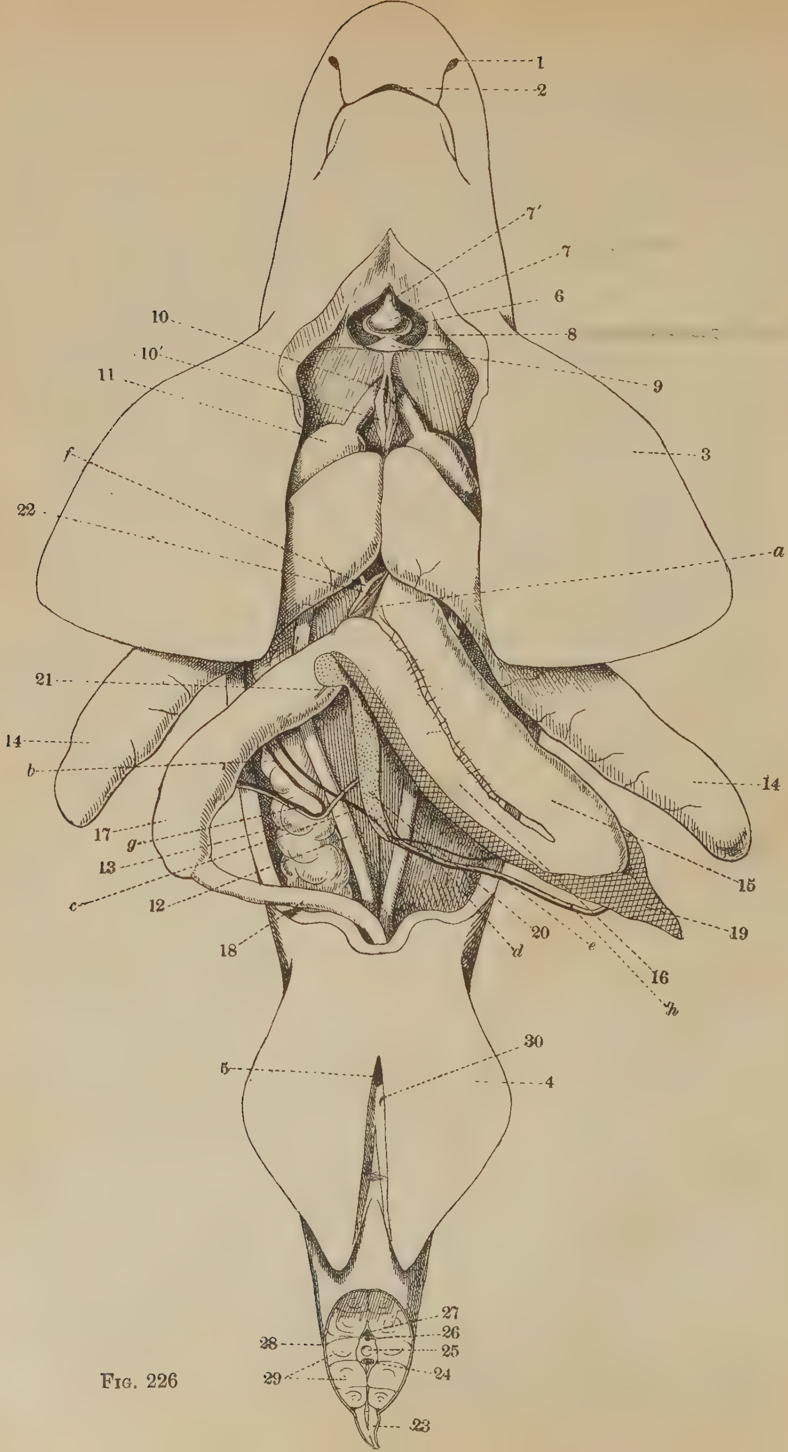
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Fig. 226

FIG. 226. *Scyllium canicula* ♀. Ventral view of viscera.

1. Left naris. 2. Mouth. 3. Pectoral fin. 4. Pelvic fin. 5. Aperture of cloaca. 6. Pericardial cavity. 7. Ventricle. 7′. Conus arteriosus. 8. Auricle. 9. Sinus venosus. 10. Coelomic opening of oviducts. 10′. Falciform ligament. 11. Shell-gland. 12. Oviduct. 13. Ovary reflected over to the right so as to show 12, which lies external to the attachment of the ovary. 14. Liver. 15. Proximal limb of stomach. 16. Distal limb of stomach. 17. Intestine. 18. Rectum. 19. Spleen. 20. Pancreas. 21. Pancreatic duct. 22. Bile-duct. 23. Dorsal fin. 24. Spinal cord. 25. Notochord in centrum of vertebra. 26. Caudal artery. 27. Caudal vein. 28. Lateral line. 29. Myotomes. 30. Abdominal pores. *a.* Hepatic artery. *b.* Intestinal branch of anterior mesenteric artery. *c.* Lienogastric artery. *d.* Gastric branch of lienogastric artery (posterior gastric artery). *e.* Splenic branch of lienogastric artery. *f.* Portal vein. *g.* Intestinal vein. *h.* Splenic vein.

kidney is the metanephros, and its tubules unite into about six main ducts, which are termed ureters. These unite with one another a very short distance from the cloaca to form a metanephric duct or common ureter. There is also a blind sperm sac into whose posterior end the vesicula seminalis opens and which immediately after receives the ureter. The compound duct thus formed meets its fellow in the middle line and so there is a single urino-genital sinus which opens into the cloaca behind the anus. In the female the mesonephros is more vestigial than in the male and its duct (the archinephric duct) is in front a very fine tube which lower down dilates and meets its fellow to form a median urinary sinus. This receives the five or six ureters on each side from the metanephros, and opens into the cloaca behind the oviduct. There is thus no common ureter in the female, and the so-called common ureter of the male is formed in quite a different way from that in which the ureter of the higher Craniata is formed (see Fig. 216, G, H).

Actual sexual congress or copulation takes place in the Elasmobranchs; the most posterior rays of the pelvic fins called the claspers are enlarged, and used to distend the cloaca of the female to allow of the entrance of spermatozoa (Fig. 227). This is correlated with the large size and small number of the eggs and their long retention in the oviduct. In the male the spermatozoa are stored in a swollen portion of the vas deferens, the vesicula seminalis, or in special pouches termed the sperm-sacs. It is probable that the claspers, the large eggs and the division of the kidney into two parts are specialisations peculiar to modern Elasmobranchs.

The Elasmobranchs are the Sharks, Dog-fish, Skates and Rays of our seas. They are almost exclusively marine and are a group

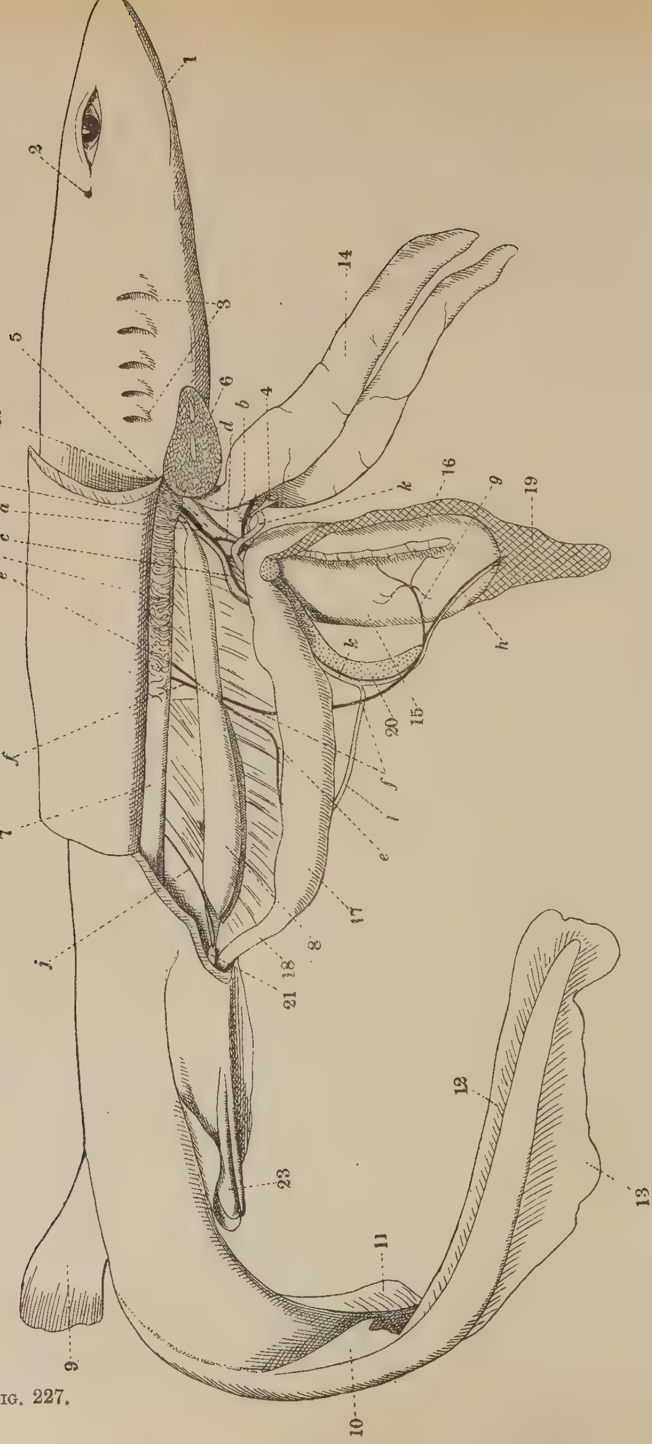
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FIG. 227.

FIG. 227. *Scyllium canicula* ♂. View of viscera from the right side.

1. Mouth. 2. Spiracle. 3. Gill-slits. 4. Gall-bladder. 5. Oesophagus. 6. Pectoral fin cut off. 7. Vesicula seminalis lying on metanephros. 8. Testis. 9. Anterior dorsal fin. 10. Posterior dorsal fin. 11. Median ventral fin. 12. Dorsal lobe of caudal fin. 13. Ventral lobe of caudal fin. 14. Right lobe of liver. 15. Proximal limb of stomach. 16. Distal limb of stomach. 17. Intestine. 18. Rectum. 19. Spleen. 20. Pancreas. 21. Rectal gland. 22. Bile-duct. 23. Claspers. 24. Ligament carrying the vasa efferentia. 25. Vas deferens. *a.* Coeliac artery. *b.* Hepatic artery. *c.* Anterior gastric artery. *d.* Pancreatic branch of the coeliac artery. *e.* Anterior mesenteric artery. *f.* Lienogastric artery. *g.* Posterior mesenteric artery. *h.* Splenic artery and vein. *j.* Posterior mesenteric artery. *k.* Portal vein. *l.* Intestinal vein.

much detested by fishermen, since they are excessively voracious and their flesh is of little value. Since the beginning of the war, however, the public taste has become more liberal and Elasmobranchs are now largely consumed both in England and also in America where they are known to the trade as "gray fish."

They are divided into two sub-orders, the Selachoidei and the Batoidei. The first consists of powerful swimmers with cylindrical bodies, well-developed tail fins and moderate pectoral fins; the latter are ground fish with broad backs and bellies and narrow sides, whip-like tails with rudimentary tail fins, and enormous pectoral fins extending forward to the extreme end of the snout.

Classification.

The SELACHOIDEI are known as Dog-fishes or Sharks, according to their size. The common English Dog-fish, *Scyllium canicula*, is about two feet long (Figs. 226, 227, and 228); another kind, the Spiny Dog-fish, *Squalus acanthias*, is distinguished by having a spine, which is merely an enlarged scale, in front of each of the two dorsal fins. *Squalus acanthias* is very common on the Atlantic coast of North America, where it is known as the Spiny Dog-fish. The American Smooth Dog-fish, *Galeus canis*, is distinguished from *Scyllium* by being viviparous. Amongst the Sharks the most remarkable are *Zygaena*, the Hammerhead, in which the roofs and floors of the orbits are produced outwards, so that the eyes are set as it were on peduncles; and *Carcharodon*, the great White Shark, which has lost its spiracles and possesses a tail-fin with crescentic under lobe. Owing to their powerful swimming capacities, Sharks are as a rule not limited in distribution. *Carcharodon* is the dreaded man-eater of the Adriatic and the warmer seas everywhere. *Zygaena* occasionally carries terror into the bay of Naples, and species of both genera are found off the American coast. The Notidanidae are a family with many interesting traits. They possess one (*Hexanchus*) or two (*Heptanchus*) extra gill-clefts, and the upper jaw directly articulates with the skull

living representatives of this family have been found in the Lias shales of England. The Port Jackson Shark of Australia *Cestracion*, is the sole surviving type of another family (the Heterodontidae),

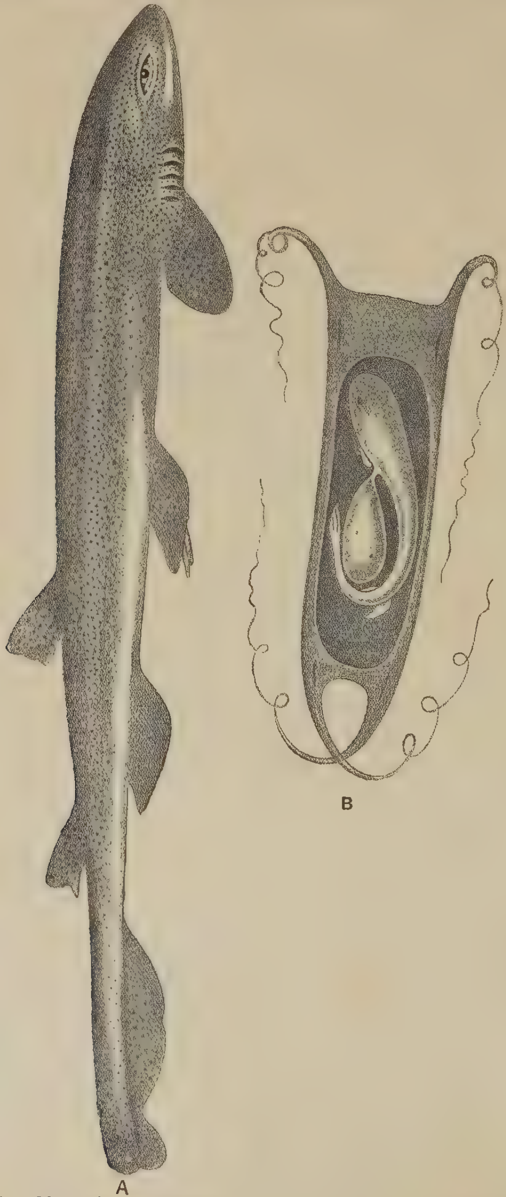


FIG. 228. A. *Scyllium canicula*. Reduced. From Day. B. Egg-case opened to show young embryo with yolk sac.

representatives of which are common in the Coal Measures. In it the snout is reduced so that the mouth is thrust forward and the jaw is attached to the skull in front of the orbit. The teeth are flat and pavement-like and adapted for crushing the Molluscs on which the animal feeds.

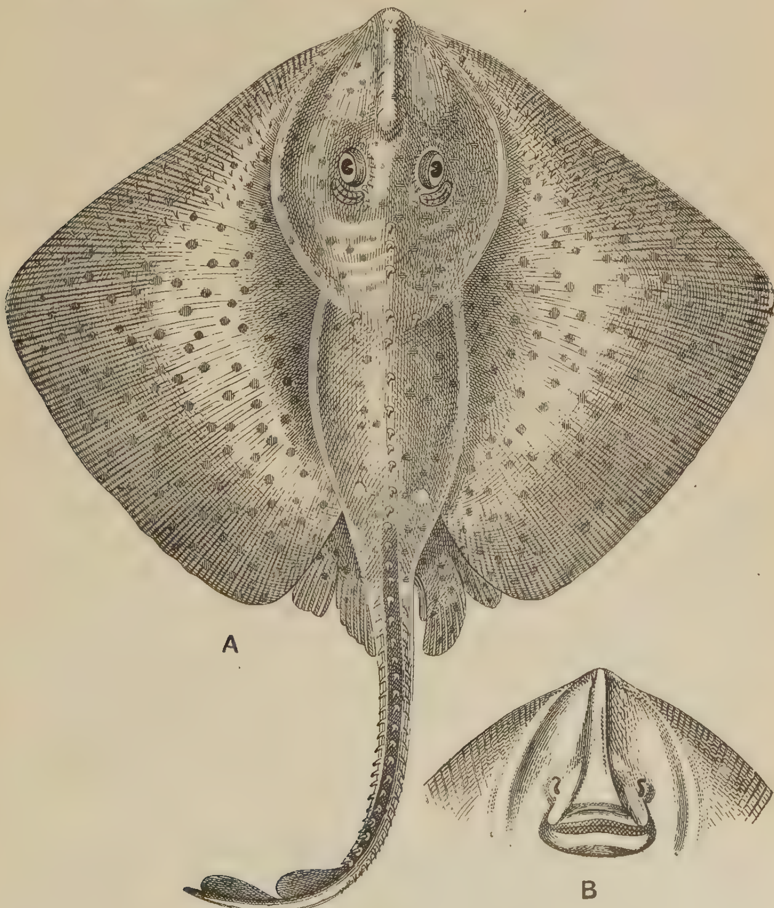


FIG. 229. *Raia maculata*. From Day.

A. Dorsal surface, showing the spiracles just behind the eyes. Reduced.
B. View of mouth and olfactory pits.

The BATOIDEI or Rays are, as we have said, ground feeders. All have the true gill openings on the underside of the body: the spiracle alone opens on the dorsal side and is enlarged. It has

in fact in this group taken on the function of pumping water into the pharynx, a duty which cannot be conveniently undertaken by the mouth when this is burrowing in the mud at the bottom. *Raia* is the common skate on both sides of the Atlantic: it has no caudal fin but two dorsals. *Torpedo* is distinguished by a more elongated body. The muscles on either side of the head are converted into electric organs, consisting of batteries of vertical hexagonal tubes filled with a clear gelatinous fluid, each tube representing a metamorphosed muscle-fibre. By means of these organs it can inflict a severe shock on its enemies. *Trygon* is the sting-ray. In it the tail is long and thin and the dorsal fin-rays are practically absent, but at the spot where the tail merges into the body there is a large recurved spine, at the base of which is a poison gland, so that by a blow of the whip-like tail it can inflict a severe wound. The pectoral fins are joined in front of the snout. *Pristis* is the saw-fish. It has an immensely elongated rostrum, at the sides of which large pointed teeth are set; the body is elongated, but it shows all the essential features of the Batoidei. The teeth in the mouth, like those of other Batoidei, are flattened, but the saw-fish is an active predaceous fish and not a bottom feeder; it is in fact a Batoid which is assuming the habits of a Selachoid. *Pristis* is found both in the Mediterranean and Caribbean Seas and elsewhere. In some of the extinct representatives of the family the upper jaw is directly attached to the cranium behind the orbit. This variation in the place of attachment indicates that the connection between the two structures is secondary.

The two most interesting fossil representatives of the Elasmobranchii are *Cladoselache* and *Pleuracanthus* whose fins are described above (p. 460).

Order II. **Holocephali.**

The second order of Chondrichthyes, the Holocephali, differ from Elasmobranchs chiefly in the skeleton; in the viscera they resemble them very closely. The Holocephali are distinguished by having the upper jaw completely confluent with the cranium, a condition called autostylic (Fig. 230): the orbits are so deeply indented that the brain is pressed back from between them, and their two cavities are only separated by a vertical plate of cartilage, called the interorbital septum. There is no spiracle and the last gill-cleft is also closed. A fold of skin, called the operculum, extends back over

the gill-slits. The gills are, however, still borne on the walls of sacs, but these are much shallower than the gill-sacs of Elasmobranchii. The snout or prae-oral part of the body is much reduced in size and supported only by a single rod of cartilage.

The scales have almost entirely disappeared and are represented only by the great spine, the so-called icthyodorulite, which stiffens the front edge of the dorsal fin, by the teeth and by the prickles on a peculiar tentacle situated on the snout of the male. The teeth are confluent, forming ridges of dentine covered with

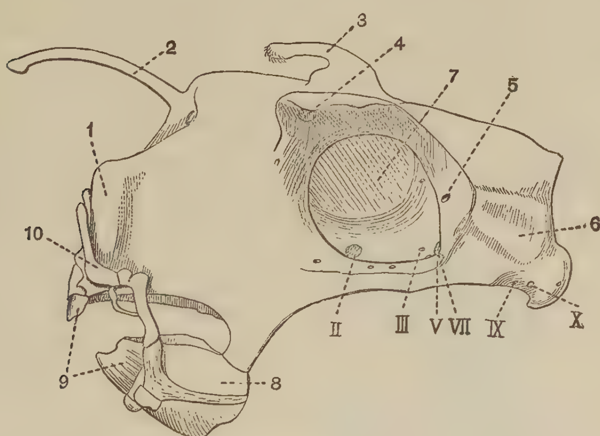


Fig. 230. Skull of a male *Chimaera monstrosa*. After Hubrecht.

1. Nasal capsule. 2. Cartilaginous appendage to the ethmoid region, representing the rostrum of Elasmobranchii. 3. Erectile appendage beset with placoid scales. 4. Foramen by which the ophthalmic nerves leave the orbit. 5. Foramen by which the ophthalmic branch of the Vth nerve enters the orbit. 6. Auditory capsule. 7. Interorbital septum. 8. Meckel's cartilage articulating with an outgrowth from the posterior part of the palato-pterygo-quadrate cartilage. 9. Teeth. 10. Labial cartilage. II, III, V, VII, IX, X. Foramina for the passage of cranial nerves.

enamel. Of these there are a pair in the lower jaw, called dentary plates, and two pairs in the upper, termed vomerine and palatine plates respectively, placed one behind the other. Each plate has certain areas, where the dentine is especially thickened, called tritors. The arrangement of these tritors is used in classifying the fossil species. The peculiar tentacle on the head of the male (3, Fig. 230) arises from a pit situated in the middle line of the snout, and bears sharp tooth-like scales at its tip, and is used to grip the dorsal fin of the female during copulation.

The notochordal sheath is not broken up into centra, but in *Chimaera* it has developed within it a large number of calcified rings, three to five times as numerous as the neural arches.

FIG. 231. *Chimaera monstrosa*, L. Male with process on snout. Reduced.

The Holocephali were once a numerous group; now they are represented by a few genera, of which the best known is *Chimaera*, sometimes called the Rabbit-fish, common to the Mediterranean and to the Atlantic coast of Europe and Africa. *C. monstrosa* is found on the east coast of N. America. On the Pacific coast *C. collei* occurs in such numbers as to be a serious nuisance to fishermen. It eats the baits off their lines. It is known as the Rat-fish, in allusion to the shape of the tail. *Callorhynchus* occurs in the temperate waters of the Southern Hemisphere. A third genus, *Harriotta*, is a deep-sea form, and quite recently another deep-sea genus *Rhinochimaera* with an enormously developed rostrum has been found off the west coast of Ireland just on the slope where the shallower inshore water passes into the abysmal depths of the Atlantic.

From the character of their dentition one would naturally conclude that the Holocephali normally fed on food which required a good deal of mastication, and if this be so we can

understand the "holostylic" modification of the skull, for it is an obvious advantage to have the upper jaw firmly fixed if the fish has to bite firmly and strongly. The loose hyostylic arrangement on the contrary is connected with mobility in the upper jaw, which indicates a capacity to enlarge the gape to a great extent and thus to swallow prey whole.

Sub-class II. Osteichthyes.

The Bony Fish constitute an enormous group; they include over 10,000 species as against about 400 species of Chondrichthyes. Of these 10,000, the overwhelming majority though divided into families differing in minor points are obvious modifications of one well marked type with which we shall become better acquainted immediately, and which is known as the Teleostean type. There remain, however, about a dozen genera including twenty or thirty species which differ from this type in important characters. These aberrant fish are in fact, highly interesting survivals of more primitive types of fish which have almost died out.

By the study of their structure we obtain some light not only on the manner in which the bony fish was evolved from a cartilaginous fish but also on the manner in which the most primitive type of land animal was derived from a fish.

For this reason a disproportionate amount of attention must be given to these aberrant forms.

They are divided into five orders, viz.

(1) the Aetheospondyli including one genus *Lepidosteus*;

(2) the Protospondyli including one genus *Amia*;

(3) the Chondrostei with four genera viz. *Acipenser*, *Scophirhynchus*, *Polyodon* and *Psephurus*.

(4) The Polypterini including two genera viz. *Polypterus* and *Calamoichthys*.

(5) The Dipnoi including three genera *Ceratodus*, *Lepidosiren*, and *Protopterus*.

All other Osteichthyes are included in one order called the Teleostei.

The Aetheospondyli, Protospondyli, Chondrostei, and Polypterini were formerly grouped together as Ganoids because *some* of them possess hard scales with a covering of shining material termed ganoin. The unsuitable character of the name is apparent when we reflect that these scales are found only in four out of the nine genera which constitute Ganoidei.

Order I. **Teleostei.**

We shall begin the study of Osteichthyes with the study of the order which includes the vast majority of living fish, viz. Teleostei. The word means the completion or perfection of bone (Gr. τέλος, end, ὀστέον, bone), and on the whole it is justified as a description of these fish. Teleostei are above all characterised by the structure of the skull and vertebral columns. In these the cartilage is largely replaced by bone developed from the modification of the connective

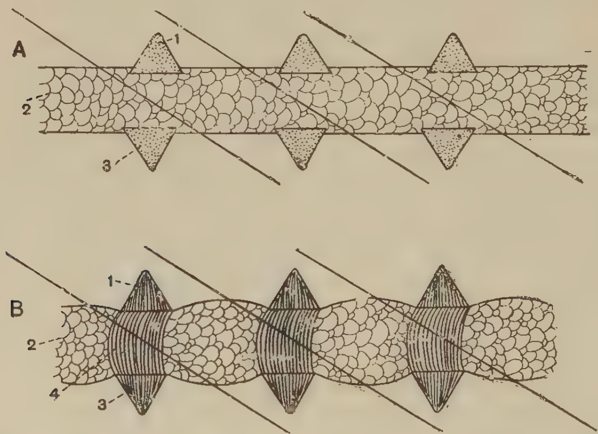


Fig. 232. Illustrating the mode of formation of the vertebral column in Teleostei.

A. Early stage in development. B. Later stage in development. The circles indicate the gelatinous tissue of the notochord, dots indicate cartilage, and close parallel lines bone. The oblique parallel lines indicate the boundaries of successive myotomes.

1. Basidorsal with neural arch. 2. Notochord. 3. Basiventral with haemal arch. 4. Bony ring connecting basidorsal and basiventral pieces and forming the centrum.

tissue around it but which eats into and replaces the cartilage, and is termed cartilage bone.

The vertebral column is composed of hour glass shaped or nearly cylindrical centra hollow at both ends, resembling in shape the centra of Elasmobranchii and like them denominated Amphicoelous (Gr. ἀμφί, both, κοῖλος, hollow), but of course composed of bone. Between two adjacent centra the notochord persists throughout life; in the young Teleostean it is continuous throughout the length of the fish but in the adult it usually becomes completely obliterated in the centre of each centrum. With each centrum

there are articulated a pair of neural arch-pieces or basidorsals meeting in a median neural spine, and constituting a neural arch enclosing the spinal cord and a pair of ventral arch pieces or basiventrals uniting in the middle line in the tail region to form a median haemal spine and so constituting a haemal arch enclosing the caudal artery and vein, but in the trunk region the haemal arch pieces do not meet: their outer ends become movably articulated with the basal pieces and constitute ribs. A centrum with its attached arches is called a vertebra. The ribs of Teleostei do not correspond to the ribs of Chondrichthyes, for whereas the ribs of that group of fish project into the midst of the myotomes, the ribs of Teleostei curve down close to the peritoneal lining of the splanchnocoel. In many Teleostei however there are curved bones termed epipleurals which spring from the basal segment of the haemal arch or basiventral and these bones correspond in position with the ribs of Elasmobranch fish and are probably homologous with them.

There are no intercalaries, either dorsal or ventral, in Teleostei.

The centra are formed by the ossification of circular bands of connective tissue outside the notochordal sheath which connect the neural arch derived from one myotome with the haemal arch derived from the one in front of it, for the myotomes slope downwards and backwards. In this way the fully formed centrum comes to lie athwart the septum dividing two myotomes, and so provides attachment for the ends of the muscular fibres derived from both myotomes (Fig. 232). In many cases a cross section of the young vertebra shows us cartilaginous neural and haemal arches projecting into a mass of bone derived from the secondary notochordal sheath. The primary sheath gives rise to neither bone nor cartilage but remains fibrous.

Turning now to the skull we find that the cranium consists of a broad ethmoid region in front and a broad occipital region behind, joined by a narrow sphenoid region between the eyes where its cavity is completely obliterated and it is reduced to a vertical plate of bone or cartilage termed the interorbital septum as in Holocephali. The cranium is at first entirely formed of cartilage as in Chrondrichthyes, and, as in that group, there is a membranous hole in the roof called the anterior fontanelle: but the cartilage becomes covered with bone which partially or entirely replaces it. In the posterior aspect of the skull there is the foramen magnum or large hole through which the spinal cord passes to join the brain. Around this are four bones, a supra-occipital with a great median crest above, an exoccipital at each end, and below

a basi-occipital which ends in a concavity resembling the end of one of the centra. The base of the interorbital septum is gripped by a Y-shaped bone called the basisphenoid and above it in the septum are developed alisphenoids behind and sometimes but not always orbitosphenoids in front.

The ethmoid region is ossified by a median mesethmoid bone in the mid-dorsal line by two lateral parethmoids one at each side.

No part of the cartilaginous nasal capsule is replaced by bone, but the auditory capsule is ossified by no less than five bones, whilst its inner wall which separates it from the cranial cavity is reduced to membrane. The bones which ossify its outer wall are (1) a pro-otic in front and below, (2) a sphenotic in front and above spreading into and partly ossifying the interorbital septum as well,

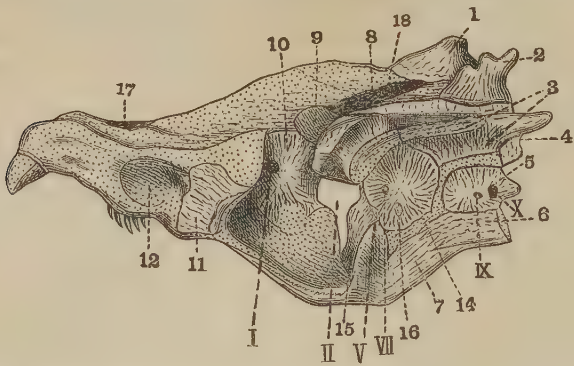


FIG. 233. Lateral view of the cartilaginous cranium of a Salmon, *Salmo salar*. After Parker. A few membrane bones are also shown. Cartilage is dotted.

1. Supra-occipital. 2. Epi-otic. 3. Pterotic. 4. Opisthotic. 5. Exoccipital. 6. Basi-occipital. 7. Parasphenoid. 8. Sphenotic. 9. Alisphenoid. 10. Orbitosphenoid. 11. Ectethmoid. 12. Olfactory pit; the vomerine teeth are seen just below. 14. Pro-otic. 15. Basisphenoid. 16. Foramen for the passage of an artery. 17. Anterior fontanelle. 18. Posterior fontanelle. I, II, V, VII, IX, X. Foramina for the passage of cranial nerves.

(3) an epi-otic above on the upper surface of the capsule usually produced in a pyramidal projection, (4) a pterotic running horizontally along the outer surface, and affording an articular surface for the second visceral arch, and finally (5) an opisthotic forming the hinder wall of the capsule (Figs. 233, 234).

The skull of the Teleostean fish is usually described as hyostylic because the upper part of the second visceral arch is developed into a hyomandibular element in order to support the hinder part of the first visceral arch as in most Elasmobranchii, but the front part of the first visceral arch has a direct articulation with the skull in the

ethmoid region and so a better name for the skull would be amphistylic. The upper half of the first visceral arch is ossified in front by a palatine bone usually bearing teeth which articulates with the parethmoid; in its central portion by three bones, viz. an ectopterygoid below and on the outer side, an entopterygoid on the inner side, and a metapterygoid above; behind where it articulates with the lower half of the arch (which forms the lower jaw) it is ossified by the triangular quadrate bone. In the lower jaw

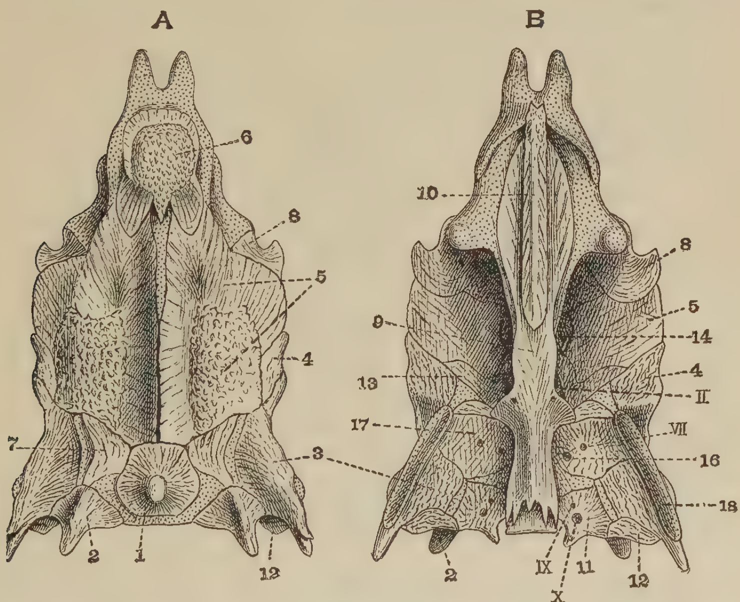


FIG. 234. A. dorsal and B. ventral view of the cranium of a Salmon, *Salmo salar*, from which most of the membrane bones have been removed. After Parker. Cartilage is dotted.

1. Supra-occipital. 2. Epi-otic. 3. Pterotic. 4. Sphenotic. 5. Frontal. 6. Median ethmoid. 7. Parietal. 8. Lateral ethmoid. 9. Parasphenoid. 10. Vomer. 11. Exoccipital. 12. Opisthotic. 13. Alisphenoid. 14. Orbitosphenoid. 16. Foramen for passage of an artery. 17. Pro-otic. 18. Articular surface for hyomandibular. II, VII, IX, X. Foramina for the passage of cranial nerves.

there is developed an articular bone which ossifies its hinder part and articulates with the quadrate.

The second visceral arch termed the hyoid is divided as in Elasmobranchii into two regions—an upper, which articulates with the auditory capsule above and is firmly attached to the quadrate region of the first visceral arch below, and a lower which swings

downwards and is united to its fellow in the mid-ventral line by a median piece or copula.

The upper segment is ossified by the hyomandibular bone above, which articulates with the pterotic, and the symplectic below, which is firmly joined to the quadrate. The lower segment begins with a small cylindrical interhyal bone to which succeeds an epiceratohyal, then the main part of the arch is ossified by a great curved ceratohyal which slants forward and downward. Beneath this is the small hypohyal which is joined to its fellow by the

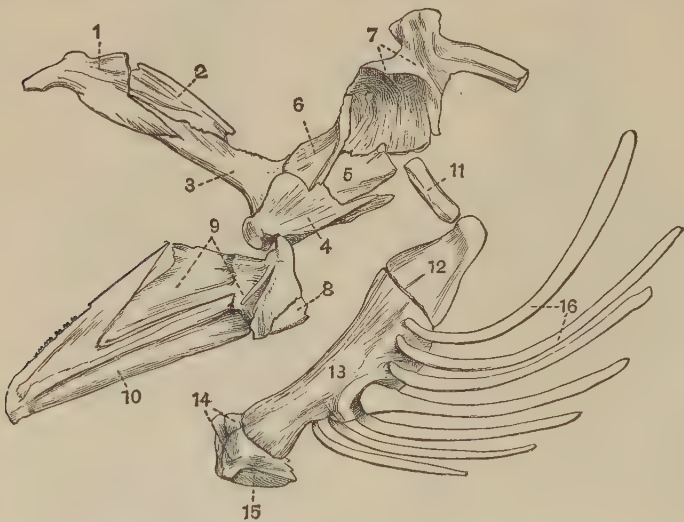


FIG. 235. Mandibular and hyoid arches of a Cod, *Gadus morrhua* × ½.

1. Palatine. 2. Entopterygoid. 3. Pterygoid. 4. Quadrate. 5. Symplectic. 6. Metapterygoid. 7. Hyomandibular. 8. Angular. 9. Articular. 10. Dentary. 11. Interhyal. 12. Epihyal. 13. Ceratohyal. 14. Hypohyal. 15. Glossohyal. 16. Branchiostegal rays.

median glossohyal which forms the copula or connecting piece between the two sides of the arch. The succeeding visceral arches are called branchial because they bear the gills. These arches are segmented in the same way as the hyoid. Each begins above with a bone termed the pharyngobranchial which frequently—indeed typically bears teeth, and which extends horizontally inwards towards the mid-dorsal line in the dorsal wall of the pharynx. The pharyngobranchials collectively are sometimes termed the superior pharyngeal bones. The pharyngobranchial is succeeded by a

knee-like piece the epibranchial. The main portion of the arch is ossified by the great curved ceratobranchial which slopes downwards and forwards. Below this is the hypobranchial which is joined to its fellow by the median copula piece, the basibranchial; this piece connects the ventral ends of all the arches together. The seventh and last visceral arch (or fifth branchial) consists of a single bone on each side lying in the ventral wall of the pharynx and bearing teeth. Since the arches slope downwards and forwards, it comes about that the teeth borne by this rudimentary arch bite against the teeth borne by the pharyngobranchials of the preceding arches, and most of the chewing of a Teleostean fish is done in this way by the action of the constrictor muscles of the pharynga which bring these two sets of teeth together. This last arch is frequently spoken of as the inferior pharyngeal bone (Fig. 235).

Besides the bones which we have described which eat into and replace the primitive cartilage there are others termed dermal bones, which are derived from the ossification of the dermis, and these we must now describe. Since the dermis forms an undivided covering for the whole head and is continuous with the lining of the stomodaeum it is impossible to assign dermal bones to definite regions of the skull such as cranium, sense capsules and visceral arches. They are better classified as (*a*) roofing bones, (*b*) bones of the lips and cheeks, and (*c*) bones of the roof of the buccal cavity or stomodaeum. To this category would have to be added in some archaic Osteichthyes, but not in Teleostei, (*d*) bones of the under side of the throat. Outside the region of the skull we find in Teleostei a series of membrane bones covering the pectoral girdle.

The roofing bones of the Teleostean skull are a pair of parietal bones lying at the sides of the supra-occipital and covering two membranous window or posterior fontanelles in the cartilaginous roof of the cranium. In front of these come a pair of frontal bones which extend forwards above the interorbital septum and join the mesethmoid, and lastly a pair of small curved nasal bones lying at the sides of the mesethmoid above the nasal capsule. The bones of the cheeks and lips in the Teleostean skull are comparatively numerous. In the upper lip there is a premaxillary bone in front bearing teeth, behind this a maxillary bone usually toothless but bearing teeth in primitive Teleostei like the Salmon, and occasionally a small jugal bone behind this again where upper and lower lips meet. In the lower lip there is

a large dentary bone bearing teeth, the hinder part of which is forked and ensheaths the articular bone, a cartilage bone already described. Beneath the articular lies an angular bone. Behind the lip bones a circumorbital chain of membrane bones extends round the lower part of the eye. The first of these is larger than the rest and is usually termed the lachrymal. Behind the circum-orbital chain we come to the membrane bones which stiffen the

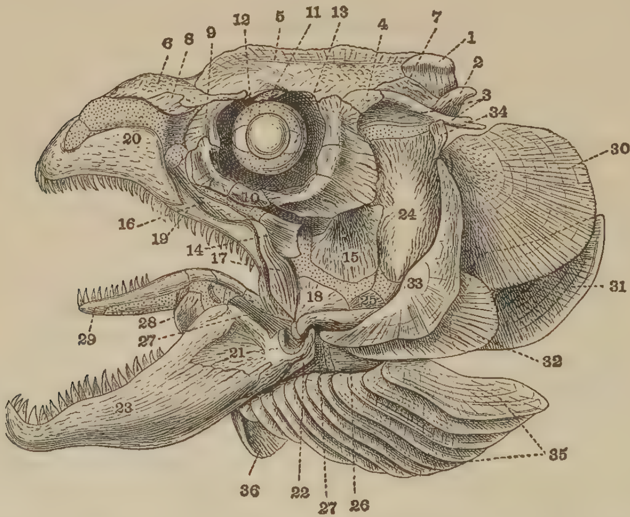


FIG. 236. Lateral view of the skull of a Salmon, *Salmo salar*. After Parker. Cartilage is dotted.

1. Supra-occipital. 2. Epi-otic. 3. Pterotic. 4. Sphenotic. 5. Frontal. 6. Median ethmoid. 7. Parietal. 8. Nasal. 9. Lachrymal. 10. Suborbital. 11. Supra-orbital. 12. Cartilaginous sclerotic. 13. Ossification in sclerotic. 14. Entopterygoid. 15. Metapterygoid. 16. Palatine. 17. Jugal. 18. Quadrate. 19. Maxilla. 20. Pre-maxilla. 21. Articular. 22. Angular. 23. Dentary. 24. Hyoman-dibular. 25. Symplectic. 26. Epihyal. 27. Ceratohyal. 28. Hypohyal. 29. Glossohyal. 30. Opercular. 31. Subopercular. 32. Infra-opercular. 33. Pre-opercular. 34. Supratemporal. 35. Branchiostegal rays. 36. Basibranchiostegal.

operculum, that is the fold of skin which, as in Holocephali, arises from the second visceral or hyoid arch and covers the gill-slits. The most anterior of these bones is the long curved pre-operculum lying just behind the symplectic; behind this is the opercular bone. Beneath it is the suboperculum, and beneath this again the interoperculum. The lower part of the opercular flap remains comparatively flexible and is stiffened by a series of

curved bones termed branchiostegal rays, which are attached to the ceratohyal and extend into the opercular membrane like the ribs of an umbrella (Fig. 236).

The bones of the palate are a single vomer in front bearing one or more transverse rows of teeth, and behind it a single bone, the parasphenoid, which underlies the base of the whole cranium, and extends backwards beneath the basi-occipital bone (Fig. 236).

We have now described the bones in a typical Teleostean skull, which is by far the most complicated skull with which we shall have to deal, and the reader may observe that any skull can be described with comparative ease and simplicity by adopting the plan which we have followed, i.e. first analysing the skull into cranium, sense capsules, and visceral arches, and describing the bones which ossify these, and then classifying the membrane bones under the categories of roofing bones, cheek and lip bones, and palatal bones.

Next to the skull and vertebral column of a Teleostean fish, the most characteristic feature of its anatomy is illustrated by the median fins. These fins have the pterygiophores or central supports divided into segments and converted into bone. Small distal segments termed baseosts lie in the bases of the fins themselves, and deeper segments called axonosts or fin-radials are embedded in the body of the fish. The fin-radials or axonosts of Teleostei are long bones, sometimes termed interspinous bones; they correspond in number and arrangement with the neural and haemal spines of the vertebrae opposite them, and they are connected with these spines by ligaments.

The tail fin or caudal fin consists of two symmetrical lobes, a dorsal and a ventral, and is of the type termed homocercal in order to distinguish it from the unequally lobed tail fin termed heterocercal, which is characteristic of the Chondrichthyes. Investigation of the development of Teleostei shows that the two lobes of this homocercal tail correspond to the ventral lobe of the heterocercal tail. The tail fin of a larval Teleost passes through a heterocercal stage, and the notochord is bent upward and passes into the upper lobe, but as development proceeds this upper lobe becomes smaller and smaller and finally disappears, whilst the ventral lobe increases in size and becomes divided into two lobes. The fin radials of the ventral lobe coalesce with the corresponding haemal spines to form one or two broad wedge-shaped bones termed the hypurals, which afford a firm base for the expanded ventral lobe now forming the whole of the tail fin. The dorsal and ventral (or,

as it is usually termed, the anal) median fins are stiffened by bony dermal fin-rays, their extreme tips alone are supported by horny rays or ceratotrichia. The dermal rays have been shown by Goodrich to be nothing more than series of thin dermal bones covering both sides of the skin flap which constitutes the fins. When a longitudinal series of them are fused together they form a "spiny" or "hard" fin-ray; when this does not take place they give rise to a jointed or "soft" fin-ray. The dermal fin-rays are

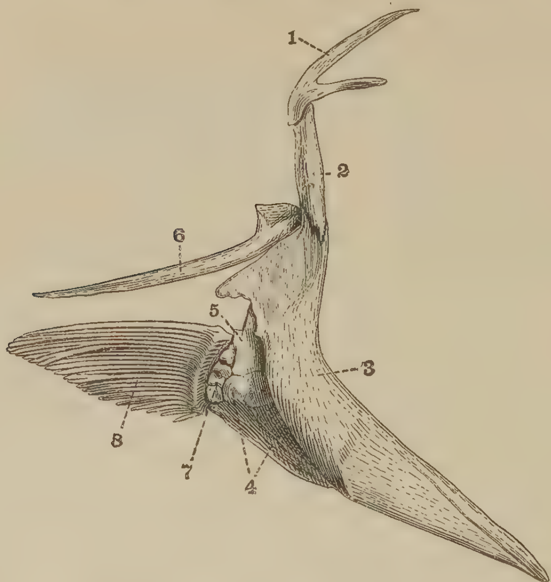


FIG. 237. The right half of the pectoral girdle and right pectoral fin of a Cod, *Gadus morrhua*, × ½.

1, 2. Supraclavicle. 3. Cleithrum. 4. Coracoid (Hypocoracoid). 5. Scapula (Hypercoracoid). 6. Postcleithrum. 7. Ossified radialia of the fin. 8. Dermal fin-rays.

termed by Goodrich "lepidotrichia." The paired fins are as a rule much less developed than in Chondrichthyes. They are stiffened by lepidotrichia and ceratotrichia just like the unpaired fins, and the pectoral fin is supported by three or four baseosts embedded in its base which correspond to the cartilaginous basalia in the pectoral fins of Chondrichthyes. Baseosts are often absent from the pelvic fin, the dermal rays of which articulate directly with the pelvic girdle. The pectoral girdle is a degenerate structure, it consists of two small plates of cartilage which are very far separated from one

another in the mid-ventral line. Each half of the girdle is ossified by two bones, a scapula above (sometimes called the hyper-coracoid) and a coracoid (sometimes termed the hypocoracoid) below. In fact, the real fulcrum for the play of the fin is not afforded by the vestigial girdle but by a series of overlying membrane bones to which the girdle is attached. This chain begins above with a forked post-temporal bone attached to crests on the epiotic and supra-occipital bones of the skull, then follows a supra-cleithrum, then a cleithrum, a curved bony bar to the under-side of which the scapula is attached, and projecting backwards from the lower end of this a postcleithrum. This last is not always present (Fig. 237). The pelvic girdle is represented by a single bone on each side.

The well-known scales with which the bodies of Teleostei are covered are in the overwhelming majority of cases thin films of dentine which are embedded in sacs of the dermis. Originally however these scales were of essentially the same nature as the membrane bones which cover the head and the pectoral girdle, and in some of the most primitive families a layer of bone is found forming the deeper part of the scale. Such scales with or without the bony layer are termed cycloid if they have a rounded posterior border, ctenoid if the posterior border is serrated. In fossil Teleostei the scales not only had the bony layer below but they were also covered above by a layer of hard shining material called ganoin, which is structureless material exhibiting neither the lacunae of bone nor the dentinal canals of dentine. Such scales are called ganoid scales. In one family of living fish (S. American Siluroids) the scales appear to be covered with ganoin, and in these fish the surface of the scale is beset with small placoid denticles and the scales are large (probably as a result of the fusion of smaller scales), and are denominated scutes. Similar bony scutes but without the placoid denticles or the ganoin are found in some other living families of Teleostei. In many Teleostei (in the Herring family for instance) as the fish grows the scales grow by the addition of concentric rings round their edges. From an inspection of the scales it is possible to calculate the age of these fish, and this becomes of great importance when the question of fish-migration is studied. It appears probable that scales and membrane bones first arose as ossifications of the dermis the purpose of which was to connect together placoid scales or teeth, and it must be remembered that teeth are merely enlarged placoid scales lining

the stomodaeum. The circumstance that teeth are borne by the lining of the pharynx covering the pharyngeal bones is probably to be attributed to an ingrowth of ectoderm through the gill-slits.

Turning now to the internal anatomy of the Teleostei, we shall emphasise the points in which structure of a typical Teleostean differs from that of a typical Cartilaginous fish described on pp. 460—466. We shall deal first with the alimentary canal.

The gill-slits are separated from each other by narrow septa, so that they are mere slits, not sacs as in the Chondrichthyes. The spiracle has disappeared. The gills themselves are long triangular filaments set in longitudinal rows on each side of each gill-septum, or gill-arch as we may term it, and they project outwards into the cavity between the gill-cover or operculum and the gill-arches. On the anterior wall of the slit between the hyoid arch and the first branchial arch there are no gill-filaments but usually a small round red body richly supplied with blood-vessels, and termed the pseudobranch. This may be a vestige of the gill belonging to the front wall of the first gill-cleft. Some think it represents the vestigial gill of the lost spiracle.

When a Teleostean fish opens its mouth to breathe the flexible part of the opercular flap supported by the branchiostegal rays is pressed against the body and prevents the exit of water through the gill-slits. Then when the pharynx is constricted in order to drive the water through the slits, the operculum is lifted and at the same time two curtain-like folds of membrane borne by the maxillae swing out and meet, and prevent the escape of water through the mouth. If the flexible part of the operculum be called the posterior breathing valve, then the curtains may be regarded as anterior breathing valves. At the pyloric end of the stomach there are usually a large number of blind outgrowths termed pyloric caeca, and, intermixed with them and difficult to detect, a number of delicate tubules which represent the pancreas. Above the stomach lies the air-bladder, which may or may not open in the mid-dorsal line by a duct into the oesophagus or the beginning of the stomach. The intestine is long and thrown into several loops, and is devoid of a spiral valve. It opens behind by an anus which is distinct from the openings of the kidneys and genital organs.

In the male the kidney has no connection with the testis, so that the kidney cannot be divided into regions but constitutes one uniform elongated organ which opens into an elongated archinephric duct. The two archinephric ducts unite into a single median duct,

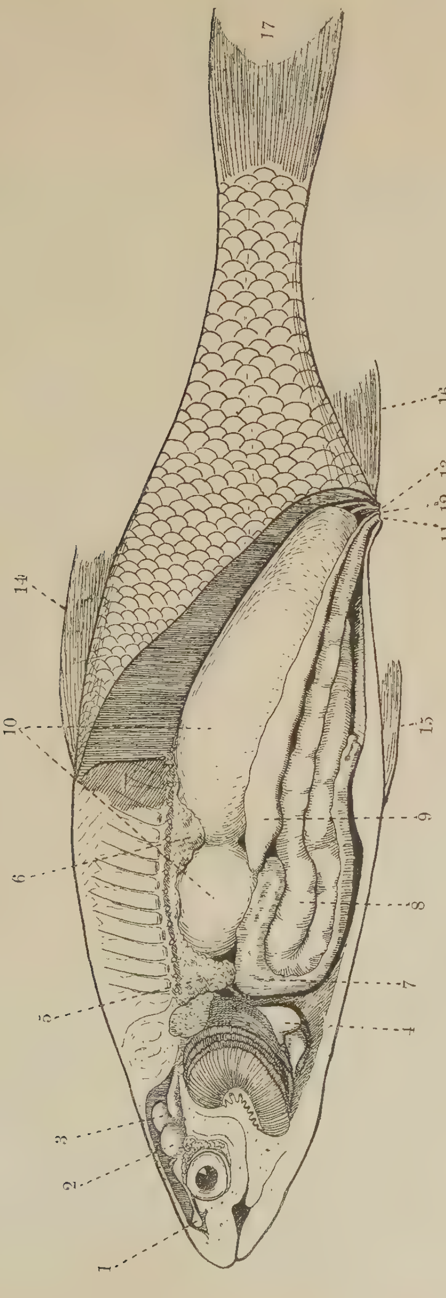


Fig. 238. A Roach, *Leuciscus rutilus*, dissected to show its brain, gills and viscera. Slightly diminished in size.

1. Olfactory lobe. 2. Right optic lobe. 3. Cerebellum. 4. Auricle of heart. 5. Lymphatic gland (the so-called head-kidney). 6. Kidney. 7. Liver. 8. Intestine. 9. Genital gland. 10. Air-bladder. 11. Anus. 12. Genital opening. 13. Opening of ureter. 14. Dorsal fin. 15. Pectoral fin. 16. Pelvic fin. 17. Caudal fin.

often swollen into a kind of urinary bladder which descends to open behind the anus by a separate opening. The testis has a duct which issues from its hinder end and unites with its fellow to open by a genital opening between the anus and the kidney opening (Fig. 238).

The researches of Prof. Kerr on some of the more archaic types of Osteichthyes have made it probable that the testis duct is to be looked on as a posterior sterile extension of the testis itself, and sections of the "duct" confirm this, because it is seen to be more of the nature of a network of tubes than a single duct. According to Jungersen it opens into the kidney duct in the embryo, and this connection may be regarded as a single posterior vas efferens; the portion of the genital duct close to the opening may be regarded as a split-off portion of the kidney duct.

In the female the ovary is similarly continuous with a short wide oviduct which joins its fellow to open by a genital opening. But in some primitive families of Teleostei, such as Salmon and Eels, the oviduct is absent and the ovary dehisces its ova into the splanchnocoel, and, as in Cyclostomata, the ova escape by abdominal pores. Investigation into development shows that the oviduct arises as a groove in the peritoneum leading to the pore, and that this groove is bounded on one side by a fold which is nothing more than a sterile extension of the ovarian ridge itself.

The brain of a Teleostean differs from that of Chondrichthyid fish (1) in the reduction of the cerebral hemispheres to their basal portions, which correspond to the so-called corpora striata in the human brain. The roof of the cerebrum is a thin sheet of non-nervous membrane continuous with the roof of the third ventricle; (2) in the solution of the optic chiasma. This, it may be remembered, is a band of nervous tissue grooved off from the floor of the thalamencephalon, in which run fibres from both eyes to both sides of the brain. In the Teleostean this is split into two separate nervous stalks each connecting one eye with the opposite side of the brain only. Since the eyes of a Teleostean fish owing to its compressed shape receive images of quite different objects, it is of no use trying to combine them; (3) in the protrusion of the cerebellum forwards into the cavity of the mid-brain as the so-called valvula cerebri.

In the cranial nerves the sole point which calls for remark is a cutaneous branch of the 5th, which is distributed to the bases of all the paired and unpaired fins where there are developed taste-buds.

The olfactory lobes are sometimes connected with the cerebrum by very long stalks (Cod family), but at other times they are sessile (most other Teleostei).

In the blood system the main difference between Teleostei and Chondrichthyes lies in the fact that in the former group the conus of the heart has disappeared as a distinct chamber, since it becomes merged in the ventricle, which has thereby become enlarged. There is only one transverse row of pocket valves, and these are situated at the origin of the ventral aorta, and correspond to the most distal pair in Chondrichthyes. The ventral aorta is thickened at its origin by an increase of fibrous tissue, but this swelling, termed the bulbus arteriosus, is not rhythmically contractile. Besides this peculiarity of the heart we find that in Teleostei the four epibranchial arteries on each side, instead of converging to join the dorsal aorta, join a ring-shaped vessel termed the circulus cephalicus, from which two posterior carotid arteries are given off in front to supply the brain and from which behind the dorsal aorta arises. The efferent branchial vessels do not form loops round the gill-clefts as in Chondrichthyes, but the efferent vessel from the hinder wall of the first cleft, i.e. the cleft between the hyoid and first branchial arches, gives off a branch which runs round the ventral end of the cleft and carries blood to the pseudobranch. From the pseudobranch blood is carried by an ophthalmic artery, which runs forward to supply the vascular choroid investment of the eye, and is connected with its fellow by a bridge above the parasphenoid. From this bridge go off arteries to the brain in front of the posterior carotids. These branches of the ophthalmic arteries are known as anterior carotids (Fig. 239).

The egg of the Teleostean fish develops into a larva which, although showing special characters in each family of the group, has certain general characters as well. Thus it possesses a continuous fin-fold in place of the separate dorsal caudal and anal fins of the adult. The notochord is at first quite unconstricted, because there are no centra, and it runs straight to its termination: the end is not bent up. Pectoral fins alone are developed, and the excretory organ is a pronephros, consisting of a single closed chamber on each side, from the inner wall of which is developed a glomerulus. From this chamber a single pronephric tubule leads into the archinephric duct. When the adult form has been attained the fish is far from having reached the adult size, and in general several years must elapse before sexual maturity is attained.

To give an account of the classification of an enormous group like the Teleostei would far exceed the limits of this book; the latest authority (Tate Regan) recognises no less than 35 primary divisions, and it would be useless, even if it were possible, for the student to memorise the characters of all these. All we can attempt to do is to give some account of some groups, mainly of those which are of economic importance, because they constitute an important source of food. Before doing so we may briefly mention

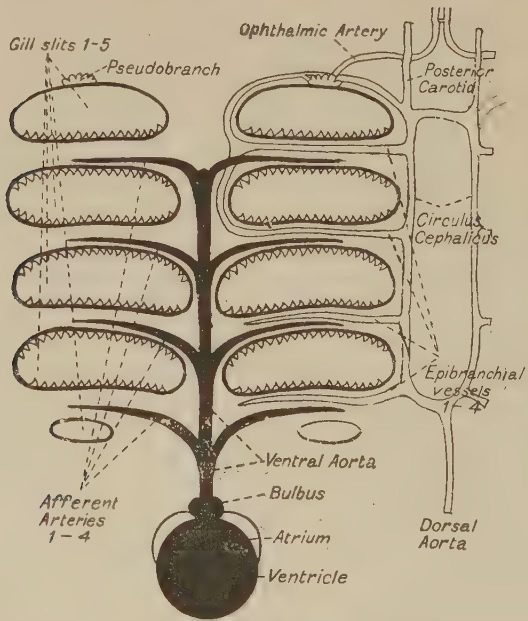


FIG. 239. Diagram illustrating the arrangement of the heart and branchial vessels in a Teleostean fish.

some of the characters which are relied on by taxonomists in dividing Teleostei into groups.

First in importance of these must be reckoned the position of the pelvic fins. In primitive forms these are placed a considerable distance behind the pectoral fins as in Chondrichthyes. This position is known as the abdominal one. But in very many Teleostei the pelvic fins are moved forward until they are immediately behind the pectoral fins and the pelvic girdle articulates with the cleithra. This position is known as the thoracic one. In some families (as for instance in the Cod family, and in the Flat-fish family) they are

moved still further forwards till the pelvic girdle is attached to the front lower end of the cleithra, and so the pelvic fins are actually in front of the pectoral. This position is known as the jugular. Next to the condition of the pelvic fins is the condition of the air-bladder. The function of this organ is to enable the fish to adjust its weight to the density of the water in which it lives. In the more primitive families the air-bladder is connected with the pharynx by a duct opening in the mid-dorsal line and the fish swallows air into its bladder. In the majority of Teleostei the air-bladder is shut off altogether from the alimentary canal and secretes its contained gases from the blood: a thickening in its wall richly supplied with blood-vessels, being termed the gas-gland. In the more primitive families the maxilla bears teeth and forms part of the gape behind the premaxilla, but in the vast majority of Teleostei the maxilla is a toothless bone embedded in the cheek and passing up behind the premaxilla. When the mouth is opened the lower end of the maxilla rotates forward and pushes out the premaxilla which is then said to be protrusible. In a large number of the more modified Teleostei certain of the lepidotrichia covering the dorsal, pectoral and pelvic fins are fused together to form hard pungent spines, and in very large groups of families, the pelvic fin possesses one such spine followed by five articulated rays. This arrangement is almost as constant as five fingers on the hands of men and monkeys.

The great sub-order Clupeiformes is characterised by abdominal pelvic fins, an air-bladder with a duct and the maxilla forming part of the gape. The coracoid has an anterior fork termed the mesocoracoid. This group includes amongst other families the Clupeidae or Herring family, and the Salmonidae (Salmon and Trout and White-fish).

The Clupeidae have a single dorsal fin and the air-bladder sends processes forward which extend into the auditory capsules and come close to the internal auditory sac, and thus this sense organ is directly affected by changes of pressure in the air-bladder. The genus *Clupea* includes the Herring, Sprat and Pilchard as well as the Shad, which is a more deep bodied form. The Anchovy distinguished by its projecting snout is *Engraulis*.

The Herring is probably the most important food-fish. It lives in comparatively deep water at a moderate distance from the coast, but comes into shallow water to spawn, its eggs being attached to stones. It is usually caught when on this spawning migration.

In spite of the enormous toll on its numbers levied by the fisheries of Northern Europe it appears to be actually on the increase. The Pilchard is a smaller fish which lays floating eggs as does also the Anchovy. The true or French Sardine is the young Pilchard. Whitebait consists of the fry of the Herring.

The Salmonidae are distinguished by having a small fin-fold devoid of rays (the adipose fin) behind the dorsal fin. The air-bladder is a simple sac and the oviducts are very short tubes unconnected with the ovary.

The genus *Salmo* includes the Salmon and Trout. *Salvelinus* is the Char (called the Trout in America) and *Coregonus* is called the White-fish in America and by various names in England. Salmon and Trout are well known as sporting fish in this country, they are esteemed as delicacies for the table but do not furnish a source of food comparable in importance with the Herring. But on the Pacific coast of America, allied genera are netted in enormous numbers, and their flesh packed in tins is sent all over the world. All the Salmonidae spawn in fresh water and the young fish passes one or two years in fresh water before going to the sea, and may (as in River Trout) pass all its life there. It is to be concluded that the Salmonidae furnish a rare instance of a family of fish primitively fresh-water, some species of which have regained the sea and are able to maintain themselves there. *Coregonus*, the White-fish of the great lakes of America and the "Pollan" of Lough Neagh in Ireland, is much esteemed for the delicacy of its flavour.

The sub-order ANGUILLIFORMES includes the Eels. In these fish the caudal and pelvic fins are lost, and the dorsal and anal fins have extended till they meet at the extremity of the tail and form a continuous fringe round the hinder end of the body. In this way a tail fin is produced which resembles that of the larva, but its apparent primitive character is due to secondary degeneration. Such a tail fin is called gephyrocercal. Scales are reduced to vestiges deeply embedded or are absent altogether. The air-bladder has a duct, and the oviducts as in the Salmonidae are represented only by abdominal pores.

In the skull the cranium is not narrowed between the orbits, the premaxilla and in some cases the maxilla is lost, and the symplectic is not developed, since the hyomandibular bone is joined directly to the quadrata. The pectoral girdle is no longer connected with the skull, the post-temporal bone being absent. Some fish belonging to this group, such as the common Eel, live partly

in the sea but periodically ascend rivers. Classed with Salmon as *anadromous* fish, the Eels in reality form a complete contrast to them—for they ascend the rivers to feed and return to the sea to spawn. They lay their eggs on the Atlantic slopes, i.e. where the drop from shallow depths to abysmal depths begins. The egg develops into an extraordinary larva termed Leptocephalus, in some ways resembling *Amphioxus*, and like it devoid of red blood corpuscles. These larvae change to minute Eels termed Elvers as thin as a wire and a few inches long, and in this condition they ascend the rivers. They leave the water and wriggle over damp grass at night in order to reach isolated ponds. It has been plausibly suggested that the Eels were originally estuarine fish and spawned close to the coast; but as the coast subsided under the sea, their original spawning place to which they have remained faithful has been buried far out under the Atlantic.

The sub-order OSTARIOPHYSI is characterised by having abdominal pelvic fins, an air-bladder with a duct, and a remarkable chain of bones on each side of the vertebral column connecting the anterior end of the air-bladder with the auditory capsule. This chain is termed the Weberian chain and it consists of a triangular bone, the "tripus," probably a modified rib, which impinges on the air-bladder, of a Y-shaped "intercalare," and finally of a cylindrical "scaphium" which rests against a membranous window in the periotic capsule. The scaphium is supposed to be the neural arch (basidorsal) of the first vertebra. The coracoid has a mesocoracoid branch and the pelvic fins are abdominal in position. This remarkable group of fish includes the families Cyprinidae (Carp, etc.) and Siluridae (Cat-fish). The former family is characterised by the presence of normal scales, and the protrusibility of the premaxilla, but the protrusibility is not effected by the motion of the maxilla. The Cyprinidae include the Carp, *Cyprinus* (species of which constitute the "gold" and silver fish), and the Roach, Loach, Gudgeon and Minnow—in fact the majority of the fish which inhabit our rivers and lakes. The Siluroids or Cat-fish derive their name from the numerous tentacle-like appendages (barbels) which adorn their mouths. One specially long one is borne by the maxilla. Certain of the fin rays of the dorsal and anal fins are developed into spines. As in Eels the brain case is unconstricted between the orbits and the symplectic is absent. Ordinary scales are never present. Either as in the Cat-fish of North America the

skin is naked, or as in the South American forms the body is covered with large shining scutes, on the surface of which are placoid denticles (Fig. 240).

The Siluridae are nearly all fresh-water, none are found in England. *Amiurus*, the Horned Pout, is a common North American fish and is eaten.

The Haplomi or Pike-like fish are characterised by possessing abdominal pelvic fins and a duct of the air-bladder, but they are distinguished from the Ostariophysi by having no Weberian ossicles and from the Clupeiformes by the fact that the pectoral girdle has no "mesocoracoid" projection.

The maxilla usually forms part of the gape. This group of normal, somewhat unspecialised fish includes the families Esocidae, with *Esox* the well-known pike, esteemed for its flavour and disliked for its destructiveness on still more valuable fish.

Fig. 240. A Cat-fish, *Amiurus catus*. Diminished. From Cuvier and Valenciennes.

The group Percesoces, as its name implies, is transitional between the sub-orders of Pike-like and Perch-like fish. The pelvic fins are always behind the pectoral and never attached to the cleithrum, but the air-bladder has no duct. This group includes the family Mugilidae in which the pelvic bones are attached to the postcleithra. The best known genus is *Mugil*, the Grey Mullet, one of the food-fish most esteemed for its flavour. As the Mullet feed on minute organisms, which are filtered from the water by strainer-like processes extending from the gill-arches, they cannot be taken by bait, but must be caught by drawing nets round the shoal, i.e. by seining.

The great sub-order Percomorphi or Perch-like fish are characterised by Tate Regan as the central group of Teleostei, for not only do they include a large number of families, but they seem to have

given rise to a good many of the groups which are now regarded as primary divisions of the Teleostei. The sub-order is characterised by the fact that the pelvic bones articulate with the cleithra, and hence the pelvic fins are thoracic or jugular in position. The air-bladder is closed, the maxilla is toothless, and there are stiff spines in the dorsal, anal and pelvic fins, except in one or two primitive families the pelvic fin has one spine and five soft rays.

Only a few of the families of this enormous sub-order can be mentioned. The Percidae, including the Common Perch, *Perca*, and the Centrarchidae, including the Black River-Bass of North America (*Micropterus*), are closely related, the first family being divided from the second by having the dorsal fin divided into spinous and soft fins, and by having fewer spines in the anal fin. The River- or Lake-Bass is one of the fish most esteemed by anglers as a sporting fish. The Serranidae closely resemble the Centrarchidae, but have one of the circumorbitals produced inwards as a shelf supporting the eye-ball. These are the Marine Perch, including the fish called in America Sea-Bass, which are highly esteemed for the table. The Mullidae or Red Mullet are distinguished by their vestigial teeth and by having two barbels; they are food-fish but much inferior in flavour to the Mugilidae. The Sparidae include the fish called the Sea-Bream, also fish of economic value distinguished from Mullidae by their large teeth, which are cutting in front and crushing at the sides. The Labridae or Wrasses are distinguished by the union of the lower pharyngeal bones in the middle line and by having pointed teeth like a dog's at the sides of the jaws. The Wrasses include many tropical fish renowned for their brilliant colours, indeed our own Wrasses assume gay colours at the breeding season. The Scombridae, or Mackerel family, are distinguished by having the spinous dorsal fin made up of a few feeble spines and by having the hinder part of the soft dorsal broken up into finlets. The body has a characteristic shape; it narrows behind so as to form a stalk for the tail fin which is greatly enlarged and deeply forked. The Mackerel, *Scomber scombrus*, is a most valuable food-fish. It occurs in shoals chiefly off the West and East coasts and is caught by seining.

The Tunny (*Thunnus thynnus*) is one of the largest of food-fish; it is 10 feet in length. It is fished chiefly in the Mediterranean and forms a valuable fishery.

The Heterosomata or Flat fish (often called the Pleuronectidae) are devoid of all rigid spines in their fins and have the

pelvic fins moved forward into a jugular position. For this reason they were formerly placed near to the Cod family, but Tate Regan has shown that they must be regarded as having sprung from the Percomorphi. One primitive genus, *Psettodes*, still possesses spines the dorsal fin. The Heterosomata derive their name from the fact that they habitually lie on one side, which is usually white, whilst both eyes are twisted on to the upper side which is deeply pigmented. The air-bladder is lost. These fish, which are captured by the trawl net which is dragged over the bottom, include a large proportion of our most valued food-fish such as the Plaice (*Pleuronectes platessa*) (Fig. 241), the Flounder (*P. flesus*), the Dab (*P.*

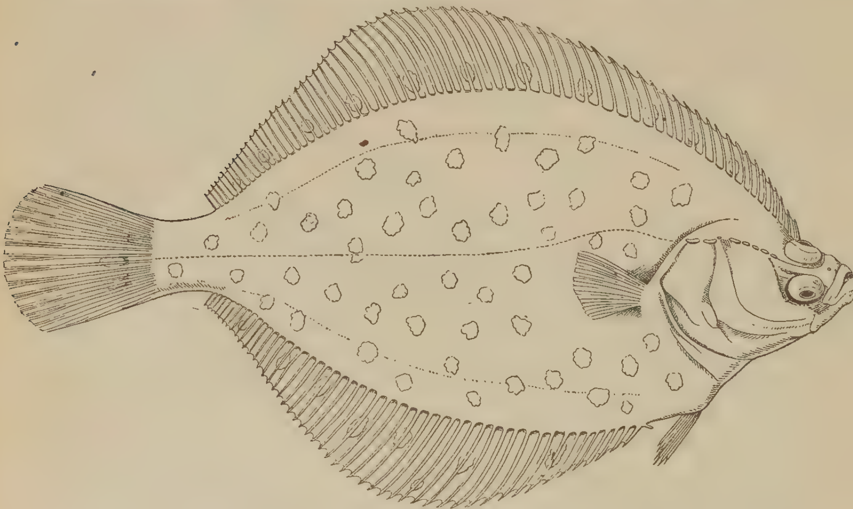


FIG. 241. *Pleuronectes platessa*, the Plaice, found from the coast of France to Iceland.

limander), the Lemon Sole (*Glyptocephalus microcephalus*), the Turbot (*Psetta maxima*), the Brill (*Psetta laevus*), the Sole (*Solea vulgaris*) and the Halibut (*Hippoglossus*), which may attain a length of 10 feet and weigh 400 lbs.

As everyone knows, the Sole is one of the most valued fish, and appears chiefly at the tables of the rich, whilst the Plaice is the food of poorer people.

The reason for this is curious: all fish owe their palatability to some peculiar chemical substance in the muscles which gives them their characteristic flavour. In the Plaice, as in most fish, the substance is present in the fish when living, and consequently unless

they are eaten just after being caught, this fugitive substance disappears and the flesh becomes comparatively tasteless. But in the Sole the characteristic flavour is only developed two or three days after death in consequence of the formation of some characteristic substance by incipient decomposition. Hence the Sole is a tasty fish even when it is brought long distances.

The GADIFORMES or Cod-like fish are fish with a peculiar mixture of primitive and secondary characters. Thus the pelvic fins are moved into a jugular position; the original tail fin supported by the hypural bones has disappeared and is replaced by a new tail fin formed by the separation of portions from the dorsal and anal fins, and supported by the neural and haemal spines. There are no spines developed in any of the fins, and the pelvic fins may have 10 or 12 rays. These features all imply specialisation, but on the other hand there is an extension of the cranial cavity forwards above the interorbital septum, and this contains the long stalks of the olfactory lobes of the brain.

This group includes the food-fish known as the Cod (*Gadus morrhua*), the Saithe (sometimes called the Coal-fish) (*G. virens*), the Pollack (termed the Lithe in Ireland) (*G. pollachius*), the Haddock (*G. aeglefinus*) and the Whiting (*G. merlangus*), the Hake (*Merlucius vulgaris*) and the Ling (*Molva vulgaris*).

The Cod, which is captured by line and bait is perhaps *the* most sought after food-fish in the world. This is due to (1) the ease with which it can be preserved in the dried condition and so carried long distances, (2) the stable and satisfying character of its flesh; it is said to be the only fish which can be eaten daily year in and year out as a staple of diet without provoking nausea.

In their pursuit after Cod the French fishermen were led further and further into the Atlantic, and this led to the discovery of Canada, and even yet the Cod-fishery attracts a population of between 20,000 and 30,000 to the desolate ice-bound shores of Labrador. British fishermen who formerly found the Hake in their own territorial waters now pursue it further and further South till they go to the Atlantic off the coast of Morocco to find it.

It is obvious that if a fishery is to be an economic success, the fish must be taken in enormous numbers at a time, and this is only possible if they are caught when they congregate in shoals. That branch of Zoology known as Fishery Science has for its object the determination of the whole course of the life history of fish of economic value, and of the causes which determine their migrations.

Armed with this knowledge Fishery Science can aid the fisherman by enabling him to find the shoals of fish, and also in some cases by protecting the fish against undue depletion of their numbers at critical periods of their lives; and in this way conserving the "harvest of the sea."

We now turn to consider the aberrant orders of Osteichthyes and the first we shall mention is the Aetheospondyli, including the single genus *Lepidosteus*, the bony Gar-Pike of the lakes and rivers of North America.

Order II. **Aetheospondyli.**

The Aetheospondyli are Ganoids, i.e. they are covered all over with bony rhomboidal scales with a shining covering of ganoin and the free edges of the scales are beset with placoid denticles. But there is no essential difference between the so-called scutes of the South American Siluroids and these ganoid scales, so that they cannot be regarded as a diagnostic character of the order. The Aetheospondyli differ from the Teleostei and agree with the Chondrichthyes in certain characters which must be regarded as archaic, i.e. derived from the common ancestor of both groups of fish. These archaic characters are (1) the testis is connected with the kidney by a series of vasa efferentia and the archinephric duct serves also as sperm duct, (2) the division of the heart known as the conus is distinct and has several transverse rows of pocket valves, (3) there is an optic chiasma containing fibres from both eyes, beneath the fore-brain, (4) there is the rudiment of a spiral valve on the intestine. The peculiar features of Aetheospondyli concern the vertebral column and the skull. In the vertebral column of the young *Lepidosteus* distinct dorsal and ventral intercalaries are present as well as basidorsals and basiventrals (neural and haemal arch-pieces). All these arch-pieces are derived from groups of cells budded from the inner walls of the myotomes, but if we consider the pieces derived from any one myotome, then the dorsal intercalary lies *behind* the basidorsal and the ventral intercalary lies *in front* of the basiventral (Fig. 242, A).

Now in discussing the vertebrae of Teleostei, we saw that the bony ring constituting the centrum connected the basidorsal of one myotome to the basiventral of the myotome in front of it.

In *Lepidosteus* the main mass of the centrum is constituted by a ring of bone connecting the basidorsal derived from one myotome with the basiventral belonging to the myotome in front. The arches

are at first cartilage, but become ossified. The dorsal and ventral intercalaries belonging to the same myotome become connected by an intervertebral ring of cartilage which constricts and finally obliterates the notochord *between* the centra. Then this ring undergoes absorption in its centre, so that a joint cavity is formed (synovial cavity) and the front half, which is concave, becomes attached to the vertebra in front and ossified, and the

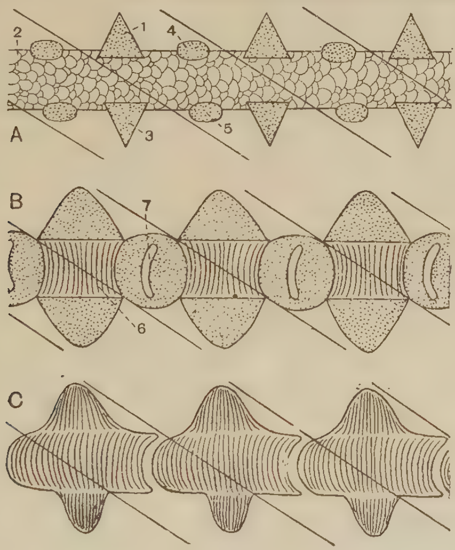


FIG. 242. Three stages in the development of the vertebral column of *Lepidosteus*.

A. Stage in which basidorsals, basiventrals, and intercalaries are all separate.

B. Stage in which basidorsals and basiventrals are connected by a bony ring, and in which the intercalaries have fused to form a cartilaginous ring in which a space, the rudiment of the synovial cavity, is appearing.

C. Stage of the completed vertebra.

1. Basidorsal. 2. Notochord. 3. Basiventral. 4. Dorsal intercalary. 5. Ventral intercalary. 6. Bony ring connecting basidorsal and basiventral. 7. Synovial cavity. Dotting, cross-hatching, etc. as in Fig. 232.

hinder half, which is convex, becomes attached to the vertebra behind, and likewise ossified, i.e. replaced by bone, so that it comes about that the vertebrae acquire articular surfaces by which they can glide on one another. If this description has been followed, it will be seen that a vertebra consists of the basidorsal and the smaller part of the dorsal intercalary belonging to one myotome, and of the basiventral and the larger part of the ventral intercalary belonging

to the myotome in front. Vertebrae which have hollow articular surfaces behind are termed opisthocoelous (Gr. ὀπισθό-, behind).

The skull is just as well ossified as that of a Teleostean, but it lacks the supra-occipital, the cartilage in that region being covered here by two dermal bones called supratemporals.

The upper jaw articulates with the pro-otic behind the eye, so that the jaw is doubly supported, since hyomandibular and symplectic are also developed, but its amphistylism is different from that of Teleostei. Covering the inner side of the lower jaw membrane bones, termed splenial and supra-angular are developed.

The tail fin is a rounded lobe derived from the ventral lobe of a heterocercal tail. The vestigial dorsal lobe is perhaps represented by a vertical line of fulcra (i.e. Λ-shaped ganoid scales), which cover its anterior border.

The jaws are long and bill-like, and the maxilla is represented by several bones in series. The fish lies in wait for its prey amidst reeds on the shallow border of lakes. Its air-bladder is produced into pockets like the alveoli of the lung of a land animal, and the fish swallows air and emits it, so that it is probable that the air-bladder is partly used as a respiratory organ.

Order III. **Protospondyli.**

The Protospondyli include, like the Aetheospondyli, only a single genus, *Amia*, represented by a single species, *Amia calva*, the Bow-fin, inhabiting the lakes and rivers of North America. The Protospondyli show the same archaic features as the preceding group in the matter of vasa efferentia, conus, optic chiasma and spiral valve; further, they have short wide oviducts opening internally into the body cavity by wide funnels, whereas in Aetheospondyli, as in most Teleostei, ovary and oviduct are continuous. The Protospondyli are, above all, distinguished by the structure of the vertebral column. In the young fish dorsal and ventral intercalaries are present as well as neural and haemal arches, and all these arch pieces become connected with each other by bony rings which form centra, but the centra so formed resemble those of Teleostei in being amphicoelous and enclosing between them portions of the notochord, and in the tail the centra are doubly as numerous as the myotomes, a centrum bearing dorsal and haemal arches alternating with one devoid of both. From the study of development it appears that the arch-bearing centrum is formed chiefly by a bony ring connecting the basi-

dorsal with the basiventral. It is termed the postcentrum. The archless centrum or precentrum is formed chiefly by a bony ring connecting the dorsal intercalaries with the ventral intercalaries. Where the tail merges into the trunk the precentrum may be seen to become attached to the postcentrum. A vertebra of the trunk consists, therefore, of the basidorsal of one myotome

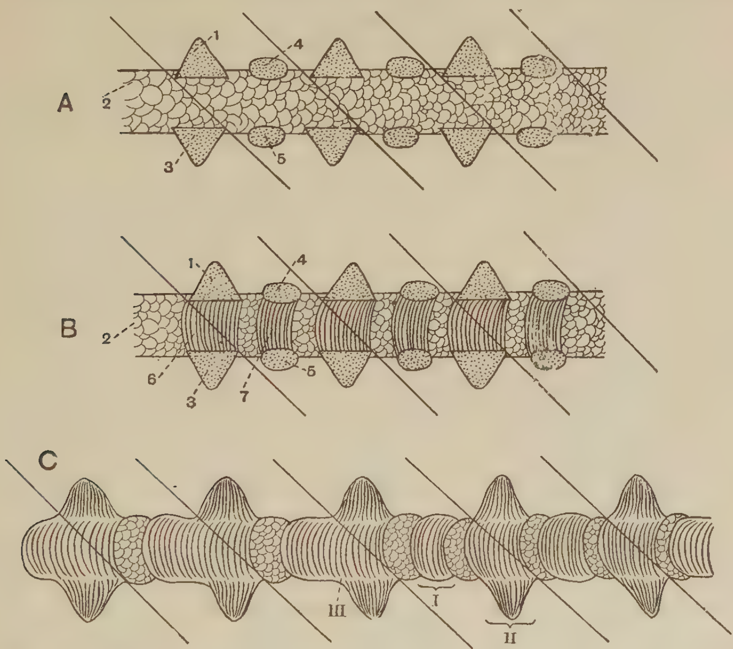


FIG. 243. Three stages in the development of the vertebral column of *Amia*.

A. Stage when basidorsals, basiventrals and intercalaries are separate.

B. Stage when basidorsals and basiventrals are connected by a ring of bone, and likewise dorsal and ventral intercalaries.

C. Stage of formation of complete vertebra in the trunk and of precentrum and postcentrum in the tail. The hinder part of the figure shows the condition in the tail, the front that in the trunk.

1. Basidorsal. 2. Notochord. 3. Basiventral. 4. Dorsal intercalary. 5. Ventral intercalary. 6. Bony ring connecting basidorsal and basiventral. 7. Bony ring connecting intercalaries. I. Archless precentrum. II. Arch-bearing postcentrum. III. Complete vertebra in the trunk. Dotting, etc. as in previous figure.

and of the basiventral and the dorsal and ventral intercalaries of the myotome in front.

The tail fin agrees in shape with that of *Lepidosteus*, but fulcra are absent, since the scales of *Amia* are "cycloid," i.e. thin and devoid of both ganoin and placoid denticles.

In the skull there is no supra-occipital, but two supratemporals occupy its place. The upper jaw is short and normal, i.e. resembles that of Teleostei, but the lower jaw has the splenial bone and in addition there is a dermal bone, the gular plate, on the under side of the throat between the halves of the jaw. The air-bladder is like that of *Lepidosteus*, and *Amia* appears to use it as an organ of respiration when the water becomes foul.

Numerous fossil fish belong to the Protospondyli, and in most cases their pre- and postcentra do not even form rings, but oblique wedges, and no complete centra are formed even in the trunk.

Order IV. **Chondrostei.**

The Chondrostei or Sturgeons include four genera divided into two families. They agree with the two preceding orders in possessing the archaic features of vasa efferentia, conus, optic chiasma and spiral valve, and the oviducts are short and open by wide funnels into the coelom.

The Chondrostei are distinguished by the condition of the vertebral column. As in the two preceding orders, dorsal and ventral intercalaries are present as well as neural and haemal arches, but only the neural and haemal arches become ossified, and that incompletely; the notochord is invested with an unsegmented cartilaginous sheath, which is a modification of its own sheath. No centra are formed. A large number of the arch-pieces are fused into a cartilaginous tube and amalgamated with the great cartilaginous cranium. The tail fin is typically heterocercal, and the front edge of the dorsal lobe is covered with a line of fulcra. The rostrum of the skull is produced into a great prae-oral snout which is used for stirring up the mud in which the fish finds the worms on which it feeds. The jaws are feeble, devoid of teeth and attached only to the skull by the hyoid arch. It is an interesting fact that not only the hyomandibular cartilage, but also some of the pharyngobranchials, articulate with the cartilaginous skull. The spiracle usually persists and has a rudimentary gill (pseudobranch) on its anterior wall. Bones replacing the cartilage are very feebly developed. In very old fish parethmoid and orbitosphenoid bones may appear, as well as pro-otics and opisthotics. In the upper jaw there is always a palatine bone and sometimes ectopterygoids, metapterygoids and quadrates, but the cartilage is merely invested—it still persists. In the second arch there is a

well-developed hyomandibular and symplectic, and the middle portions of the ceratohyals and ceratobranchials are also invested by bone.

Dermal bones are well developed both on the upper surface and sides of the head. The rostrum and occipital region are covered by numerous bones, and the typical series of paired bones on the roof of the skull may become separated by an intercalated secondary series of median membrane bones. In the upper lip a maxilla, but no premaxilla, is developed, in the lower lip a dentary bone appears. On the roof of the mouth there is in front a single bone representing the vomer, and behind it an immense parasphenoid. The region of the pectoral girdle is covered by membrane bones having in general the same arrangement as in Teleostei, but between the two cleithra there are two clavicles which meet in the mid-ventral line. These bones, absent in Teleostei, are present in most land animals, and must have been inherited from the common ancestor from which fish and land animals are derived.

Living Chondrostei fall into two families, viz. the Acipenseridae, including *Acipenser* and *Scaphirhynchus*, which possess five longitudinal rows of great bone scutes on the body, which appear to merge insensibly into the dermal bones of the head, and the Polyodontidae, in which the body is naked except for vestigial scales embedded in the skin, and there is no series of median dermal bones on the roof of the head. The dorsal lobe of the tail fin retains, however, its series of fulcra (Fig. 244).

Caviare is prepared from the ovaries

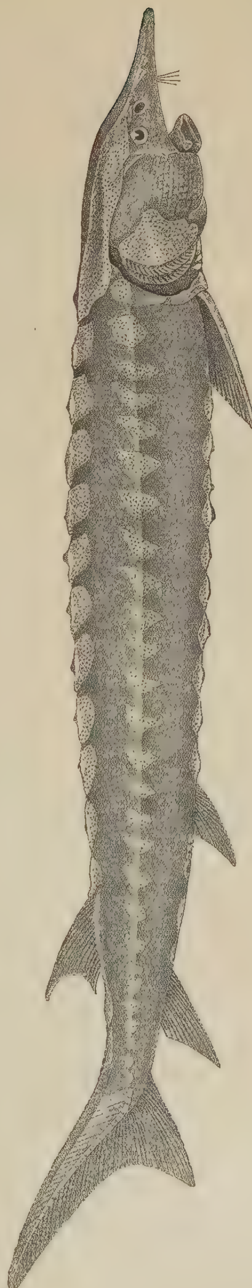


Fig. 244. *Acipenser sturio*, the Sturgeon. From Day.

of members of both families, from Polyodontidae in America and from Acipenseridae in Russia.

The Acipenseridae are, like Salmon, anadromous fish, spawning in fresh water, but, with the exception of one or two species, seeking their living in the sea. The Polyodontidae, so far as is known, are fresh-water. *Acipenser* is found occasionally off the British coast, but abounds in the rivers of Russia and the Black Sea. *Polyodon* is a denizen of the Mississippi.

To the order Chondrostei belong a large number of fossil fish, and as we recede backwards in geological times the peculiar features of the Sturgeon gradually fade out. The rostrum in older forms is shorter, a premaxilla as well as a maxilla is present, and both bear teeth (as the maxilla does in the young *Polyodon*); the body is clothed with shining "ganoid" scales, like those of *Lepidosteus* and *Amia*, and the whole animal looks very like an ordinary fish, but is destitute of an ossified backbone and, so far as is known, of cartilage bone in the skull.

These extinct fish are termed "Palaeoniscids," and in this case their evolution into Sturgeons has been a degeneration, not an advance, in structure.

Order V. **Polypterini.**

The Polypterini include two genera, *Polypterus* and *Calamoichthys*, both confined to the rivers of Africa. This order agrees with the three preceding in the archaic features of conus, optic, chiasma, and spiral valve, but it agrees very nearly with Teleostei in the character of the male organs. As in that order there is a sterile posterior prolongation of the testes consisting of a central duct with a network of sterile tubes around it, and this portion of the testes, as in the young Teleostei, communicates with the hinder portion of the archinephric duct by a single tube which may be looked on as a single posterior vas efferens. In the female the oviduct is short and opens by a wide funnel into the coelom. The Polypterini further agree with the Teleostei in the character of the vertebral column, which consists of well ossified amphicoelous vertebrae bearing two sets of ribs, viz. dorsal ribs, which correspond to the "epipleurals" of Teleostei and the ribs of Chondrichthyes, and ventral ribs, which correspond to the ribs of Teleostei and all other Osteichthyes.

The peculiarities of Polypterini are to be found in their fins

and in their respiratory organs. Thus the tail fin is a symmetrical fringe round the end of the body, and resembles the tail fin of the Teleostean larva. Such a primitive type of fin is called diphycercal. The dorsal fin is broken up into a series of finlets, each beginning with a stout spine (whence the name *Polypterus*, lit. many fins), and the pectoral fin has a median scaly lobe round which the dermal fin rays (lepidotrichia) form a fringe, whence the name Crossopterygii (lit. fringe-finned, Gr. *κροσσοί*, a fringe), which Huxley bestowed on the order. The air-bladder is deeply bilobed, the left lobe being much larger than the right one, and the two lobes unite into a median duct, which opens on the ventral side of the pharynx—an arrangement which recalls that of the lungs of land animals—and the *Polypterus*, like *Amia* and *Lepidosteus*, swallows air, which it uses for respiratory purposes, the used air escaping by the spiracle, which persists and has a little gill-cover of its own. The larva possesses a long feather-shaped external gill attached to the hyoid arch, resembling the gills borne by Amphibian larvae. Here again we see features which seem to be derived from the common ancestor of fish and land animals.

FIG. 245. *Polypterus.*

The body is covered with rhomboidal shining ganoid scales, beset with placoid denticles, like those of *Lepidosteus*. In the skull the jaws are articulated as in Teleostei; there is a hyomandibular bone, but no symplectic, and in the lower jaw a splenial bone is developed, and on the under side of the throat a pair of gular plates. The vomers are paired, and in the dermal pectoral girdle clavicles are present, as in Chondrostei. The pectoral is uniseriate with three

basals, as in Elasmobranchia. Of these the two outer are ossified, while the central one remains cartilage.

Calamoichthys is an eel-like form, but agrees in all essentials with *Polypterus*. With the Polypterini were formerly associated a large number of fossil fish common in the Devonian and Carboniferous strata, which Goodrich has separated under the name OSTEOLEPIDOTI. These agree with Polypterini in having a diphycercal tail and a scaly lobe in the pectoral fin, and in having shining rhomboid scales. It appears, however, that the pectoral fin is biseriate, of the type to be described in the next order, and according to Goodrich the scales which he terms cosmoid, have a different structure from the ganoid scales. In cosmoid scales, under a very thin layer of shining substance, there is a row of pulp-cavities from which radiate dentinal canals, suggesting that this layer of the scales is derived from the fusion of placoid denticles.

Order VI. Dipnoi.

The Dipnoi, or Lung-fish, including the genera *Protopterus* from the swamps of Africa, *Lepidosiren* from the swamps of South America, and *Ceratodus* from the Australian rivers, are distinguished

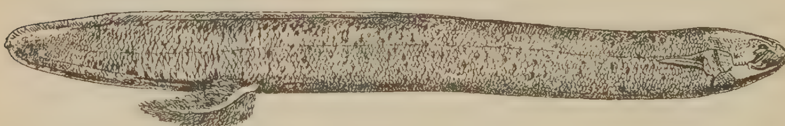


FIG. 246. *Lepidosiren paradoxa*. Male, showing the feathered pelvic fins of the breeding season. Much reduced. From Graham Kerr.

for their power of breathing air as well as water. In the case of *Lepidosiren* and *Protopterus* this is necessary, because the swamps in which they live dry up in the dry season, a time which the fish pass through buried in the mud, enclosed in air-containing chambers or cocoons which communicate with the surface by breathing-pores. *Ceratodus* inhabits rivers in which the water turns foetid at certain seasons of the year from decaying vegetation, and during this period it breathes air. The air-bladder is bilobed in *Protopterus* and *Lepidosiren*, undivided in *Ceratodus*; its walls are developed into pockets or sacculi, like those of the lungs of land animals, and the two lobes unite to form a duct which passes

to the left of the pharynx and opens into it in the mid-ventral line as in Polypterini. In *Ceratodus* a similar duct leads from the undivided sac to the pharynx. But the power of using the air-bladder to breathe air is one which is shared by the Protospondyli, the Aetheospondyli, and the Polypterini: the really characteristic features of Dipnoi are to be found in the modifications of the vascular system, which resemble closely those found in the

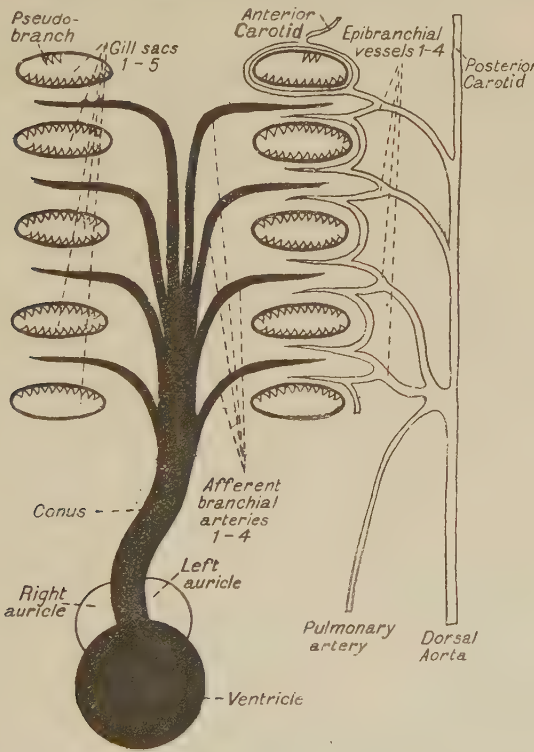


Fig. 247. Diagram of the arterial arches of *Ceratodus*, viewed from the ventral side.

lowest land animals, the Amphibia, and strongly support the view that Dipnoi in most points retain the structure of that group of fish from which land animals were derived.

Thus we find that the atrium of the heart is divided by a septum into a large right and a small left auricle, and that whereas the right auricle receives its blood from the sinus venosus, the left receives blood direct from the lobes of the air-bladder, or as we

shall term them the lungs, by two pulmonary veins. The conus of the heart is spirally twisted and contains several transverse rows of pocket valves. In *Ceratodus* one valve in each row is enlarged so as to touch one in the next row, and in this way an obliquely longitudinal valve is foreshadowed, which becomes a definite structure in *Lepidosiren* and *Protopterus*. There is no ventral aorta; the afferent branchial arteries, of which there are four or five pairs, arise in two groups—one group from the distal end of the conus, whilst the hinder group, though becoming distinct at the end of the conus, really arises from its dorsal surface some distance back. The longitudinal valve is inserted in such a way that when the free end is pressed against the wall of the conus the valve covers the openings of this hinder group of afferents. The efferent arteries are five in number on each side, each made up of a pair of vessels, one of which drains the gill on the front of the arch and one the gill on the back. The spiracle is lost, and the first cleft has a gill only on its anterior border. In *Ceratodus* this gill is a "pseudobranch," supplied by a branch from the first efferent running round the ventral edge of the cleft. The vessel which carries the blood from this gill, as in Teleostei, is a carotid artery (Fig. 247). In *Protopterus*, however, this hyoidean gill receives an afferent vessel from the ventral aorta, and its efferent joins the dorsal aorta. In this genus and in *Lepidosiren* there are no gills on the hinder wall of the hyoidean cleft, on either wall of the next cleft, and on the front wall of the third cleft, corresponding afferent and efferent vessels form one continuous "arterial arch." The arteries supplying the lungs, i.e. the pulmonary arteries, arise from a stem formed by the junction of the last two or three efferents; the first two efferents on each side form a distinct stem opening separately into the dorsal aorta.

During the contraction of the heart the oblique longitudinal valve is pressed down so as to close the entrance to the last two afferent arteries on each side. The valve is so situated that the blood which pours into the atrium from the sinus venosus is directed by it to the openings of these last two afferents, and so the bulk of it is directed to the lung, whilst the blood from the left auricle which enters the other side of the ventricle is shut off by the valve from entering the last two afferents, and goes forward to enter the first two afferents which spring from the anterior part of the conus, and so through the carotids to the head—that passing through the hyoidean gill receiving a further purification. A very similar

arrangement will be described when we come to deal with Amphibia. But the resemblance to the vascular system of land animals does not end here. The blood brought to the kidneys by the renal portals filters through them, and emerges into two subcardinal veins running along the inner sides of the kidneys. In *Ceratodus* these two subcardinals are prolonged forwards in the usual way as two posterior cardinal veins which enter the ductus Cuvieri, but a median vein, the vena cava inferior, arises by two forks from the subcardinals and passes forwards to enter the sinus venosus of the heart. In *Protopterus* and *Lepidosiren* much the same arrangement is found, but the left posterior cardinal has disappeared. Prof. Kerr, to whom more than to anyone else we owe the elucidation of the anatomy and development of these fish, suggests that the vena cava arose through the long lobe of the liver touching and effecting an adhesion with the dorsal wall of the splanchnocoel in the region of the kidneys. In this way some of the blood from the subcardinals can enter the branches of the hepatic vein, and a short road was thus provided by which it could reach the heart, and the enlargement of this channel formed the inferior vena cava (Fig. 248).

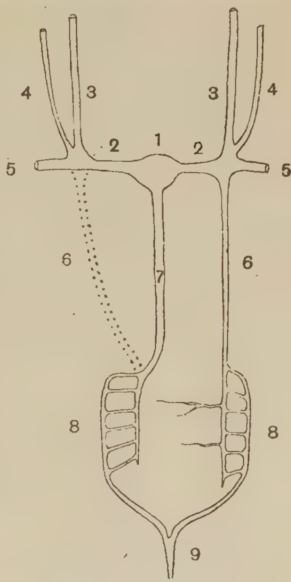
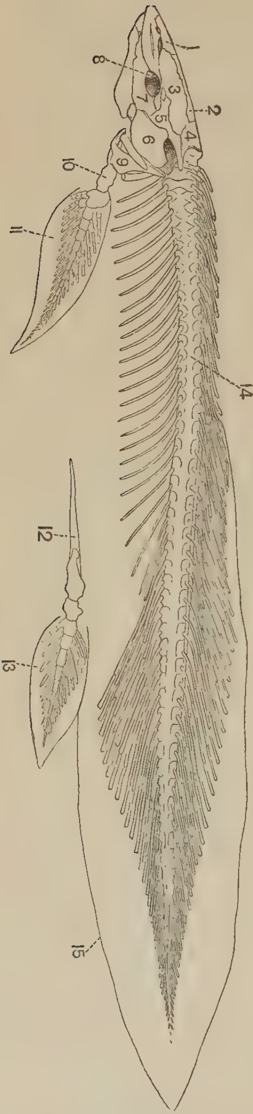


FIG. 248. Diagram to show arrangement of the principal veins in a Dipnoan.

1. Sinus venosus—gradually disappearing in the higher forms. 2. Ductus Cuvieri = superior vena cava. 3. Internal jugular = anterior cardinal sinus. 4. External jugular = sub-branchial. 5. Subclavian. 6. Posterior cardinal, front part = venae azygos and hemiazygos. 7. Inferior vena cava. 8. Renal portal = partly hinder portion of posterior cardinal. 9. Caudal. The hepatic portal system is omitted.

When we turn to the kidneys and the generative system, the researches of Prof. Kerr have brought to light an interesting series of modifications. In all three genera the oviduct opens by a funnel into the coelom, but it is much longer than in most Osteichthyes. In all three genera kidney ducts and generative ducts open with the alimentary canal into a cloaca, as in Chondrichthyes.

In *Ceratodus* the testis is connected with the kidney by a number of vasa efferentia. These arise from a longitudinal duct running



along the testis which acts as a collecting duct. A quite similar arrangement is found in the lower Amphibia as well (as already described) as in Chondrichthyes.

In *Lepidosiren* the hinder part of the testis is sterile and consists mainly of this longitudinal duct with some rudimentary tubules, and this portion alone is connected with the kidney by five or six vasa efferentia.

Finally, in *Protopterus* there is the same sterile extension of the testis, and this is connected with the kidney by a single vas efferens which joins the neck of the capsule of one of the kidney tubules. If vas efferens and tubules were simplified into a single wide tube we should reach the condition of *Polypterus*, and if this duct were split off from the archinephric duct and acquired a distinct opening to the exterior, we should reach the condition of Teleostei.

The alimentary canal has a spiral valve, as in other archaic groups of fish. The brain of *Protopterus* and *Lepidosiren* resembles that of Chondrichthyes and Amphibia in having definite cerebral hemispheres with nervous matter all round, but that of *Ceratodus* is like the brain of Osteichthyes in having only a membranous roof. The opening of the nasal sac is divided into two as in almost all Osteichthyes, but the whole sac lies, as in Chondrichthyes, on the under side of the snout, and the inner opening is within the stomodaeum, thus foreshadowing

FIG. 249. Lateral view of the skeleton of *Ceratodus miolepis*. After Günther.

1, 2, 3. Roofing membrane bones. 4. Cartilaginous posterior part of cranium. 5. Pre-opercular (squamosal). 6. Opercular. 7. Suborbital. 8. Orbit. 9. Pectoral girdle. 10. Proximal cartilage of pectoral fin. 11. Pectoral fin. 12. Pelvic girdle. 13. Pelvic fin. 14. Spinal column. 15. Caudal fin (diphycercal).

the choana or posterior nostril of Amphibia. A further resemblance to Amphibia is found in the fact that the taste-buds scattered over the body in all other Pisces are in Dipnoi confined to the region of the mouth. The eggs of *Protopterus* and *Lepidosiren* develop into larvae extraordinarily like the larvae of Amphibia but with four, not three, feathery external gills on each side attached to the gill-arches. Traces of these gills remain throughout life in *Protopterus*. We see then that Dipnoi present strong resemblances to Amphibia in the anatomy of their "soft parts," and also resemblances to primitive Chondrichthyes, and we shall be disposed to agree with Prof. Kerr that they are nearly related to the old group of fish which first migrated from the seas into the rivers and finally reached swamps liable to dry up, and became in this way adapted to life on land, and so gave rise to all land animals. Strange to say, this conclusion has been attacked by some able zoologists who, basing their conclusions on the skeleton, regard all resemblances between Dipnoi and Amphibia as deceptive. We must therefore turn our attention to the skeleton and see how far these conclusions are justified.

In the backbone of Dipnoi there are no vertebrae. The notochord is surrounded by a thick sheath which as in Chondrichthyes is transformed into cartilage by the invasion of cells derived from the cartilage forming the bases of the neural and haemal arches. These arches are partly transformed into bone, but intercalaries are absent or vestigial and developed irregularly. Neural and haemal arches are ossified. There is a diphycercal fin forming a fringe round the hinder end of the body as in Teleostean larvae and in Amphibian larvae also and there are no separate anal or dorsal fins. The paired fins are of the type called biseriate, i.e. they consist of a jointed axis of pieces of cartilage to which are attached on each side a series of jointed branches termed rays. Such fins have been found in the extinct Osteolepidoti and in the extinct Chondrichthyid *Pleuracanthus*. Such a fin is termed an archipterygium. In *Protopterus* and *Lepidosiren* the axis is developed into a long whip-like filament, and the rays are vestigial and attached only to the base of the axis.

In the skull the upper jaw is completely fused with the cranium, and the teeth in both jaws are amalgamated to form great dentary plates as in Holocephali. Only a pterygoid bone is developed in the upper jaw and premaxilla and maxilla are absent. The cranium is ossified mainly by two great exoccipital bones behind, but

orbitosphenoids are also present (Fig. 250). Of the bony plates derived from fused teeth there are two pairs which represent the vomers, and palatine bones are situated on the roof of the mouth. In the lower jaw there is a membrane bone, the dentary, which carries on each side another dental plate. But the roofing bones of the skull consist of two median bones one behind the other, flanked by a lateral bone on each side, and it appears to be mainly on this ground as also on the absence of premaxilla and maxilla that relationship to the Amphibia is denied, because in Amphibia the roofing bones form a paired series, as in most Osteichthyes, and premaxilla

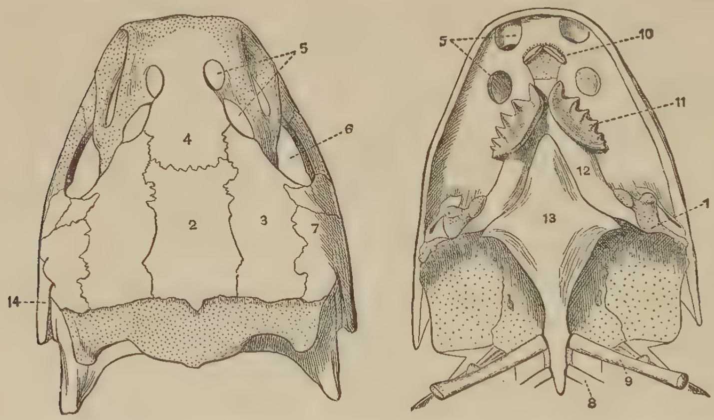


Fig. 250. Dorsal (to the left) and ventral (to the right) views of the cranium of *Ceratodus miolepis*. After Günther.

1. Cartilaginous part of the quadrate with which the mandible articulates. 2, 3, 4. Roofing membrane bones. 5. Nares. 6. Orbit. 7. Preopercular (squamosal). 8. Second rib. 9. First rib. 10. Vomerine dental plate. 11. Palatine dental plate. 12. Pterygoid. 13. Parasphenoid. 14. Interopercular.

and maxilla are present and bear teeth, and the upper jaw, though fused with the cranium before and behind, and not movable on it, is not completely fused with it. But of course the most ardent supporter of the view that Dipnoi are related to the ancestors of Amphibia would admit that it is a very long time since the two groups were separated from one another, and that modern Dipnoi have undergone changes in the meantime. As a matter of fact, when we examine fish which are regarded as fossil Dipnoi, chiefly on account of the fusion of their teeth into plates and the shape of their fins, we find that premaxilla and maxilla are present, and that the head is covered with numerous roofing bones, the most

conspicuous of which form a paired series between which a median series is beginning to appear (as happens also in *Acipenser*). We conclude therefore that these differences between Amphibia and modern Dipnoi are due to degeneration on the part of the latter and are not primitive. The gill-arches of modern Dipnoi are simple rods with at most a single joint, as in Amphibia, and the bones of the opercular flap are represented by a single bone which strongly resembles the squamosal in Amphibia in position.

The body is covered with thin scales deeply sunk in the skin. These scales have a well developed bony layer covered with dentine. The scales of extinct Dipnoi resembled those of Osteolepidoti in possessing a superficial layer of pulp-cavities covered with a thin layer of ganoin. The scales of both recent and fossil fish agree in having little solid spines covering their margins, not to be confounded with placoid denticles such as cover both margins of the scales of *Lepidosteus*, *Polypterus* and some Siluroid fish. Modern Dipnoi are divided into two suborders, viz.:

(1) Monopneumona, including *Ceratodus*, characterised by the undivided air-bladder, the well-developed archipterygial paired fins, the hyoidean pseudobranch, the complete series of gills, the membranous roof of the brain, and the fact that the young emerge from the egg like the adult.

(2) Dipneumona, including *Lepidosteus* and *Protopterus*, characterised by the bilobed air-bladder, the vestigial paired fins—devoid of fin-rays and resembling filaments—the true gill on the hyoid arch and the reduction of the other gills, the nervous roof to the brain, the fact that the larvae have external gills and the eel-like form of the adult.

Before dismissing the Pisces and passing on to consider land animals, we may endeavour to sum up the general conclusions to which our study has led us.

The most primitive fish must have resembled in many points the Chondrichthyes, as for example in possessing no bone and in having as sole skeleton the placoid denticles. The Chondrichthyes have been enabled to survive to the present day chiefly by the development of the oviduct into a womb and the great advantage which this gives in enabling them to launch their young fully equipped for the battle of life instead of turning them loose as helpless larvae as do almost all Osteichthyes. The air-bladder of Osteichthyes corresponds to the lungs of land animals and from observations on the development of lungs we are led to regard these as a posterior

pair of gill pouches the external openings of which have become lost. In *Polypterus*, *Protopterus* and *Lepidosiren* both lungs are preserved and, as in land animals, they join a duct which opens into the pharynx by a median ventral opening. In *Ceratodus* the opening is also median and ventral but there is only one lung. In the other Osteichthyes, it is probable that only one lung has been preserved but the opening has become shifted to the mid-dorsal line. Finally the circumstance that all archaic Osteichthyes use the air-bladder for respiration leads to the suggestion that the group was evolved in shallow waters near land and has since re-invaded the sea, gradually displacing its original inhabitants the Chondrichthyes.

CLASSIFICATION.

Class Pisces.

Sub-class I. Chondrichthyes. Pisces in which the skeleton is formed of cartilage strengthened by deposits of calcareous matter but in which no true bone is developed. The skin is protected only by placoid denticles composed of dentine. There is no air-bladder, the nostril is undivided and the eggs are few and large, a large part or the whole of development being completed before laying.

Order I. **Elasmobranchii.** Chondrichthyes in which there is no common gill-cover or operculum, in which the skin is covered with placoid denticles and in which the upper jaw, though it may articulate directly with the skull, is not fused with it. The notochordal sheath is segmented into distinct centra.

Sub-order 1. **Selachoidei.** Active free-swimming Elasmobranchii with cylindrical or spindle-shaped bodies in which the gill-slits are placed above the level of insertion of the pectoral fin which is of moderate size and not joined to the skull.

Ex. *Hexanchus*, *Heptanchus*, *Heterodontus* (*Cestracion*), *Scyllium*, *Squalus*, *Galeus*.

Sub-order 2. **Batoidei.** Sluggish bottom-living Elasmobranchii with flattened bodies. Openings of the gill-slits situated on the ventral surface beneath the insertion of the pectoral fin which is of great size and the front end of which is joined to the skull.

Ex. *Raia*, *Trygon*, *Pristis*.

Order II. **Holocephali.** Chondrichthyes in which there is an opercular flap springing from the hyoid arch and covering the gill-slits, in which the skin is naked, the placoid scales being restricted to the frontal tentacle of the male and to spines in front of the unpaired fins. The upper jaw is fused with the skull and the notochordal sheath is not divided into centra.

Ex. *Chimaera, Rhinochimaera, Harriotta, Callorhynchus.*

Sub-class II. OSTEICHTHYES. Pisces in which true bone is present, at least in the form of dermal plates covering the head, and of flat scales covering the body and connecting together the bases of the placoid denticles if these are present. Bone is also present in every case as a partial or complete investment of the cartilage of the skull. An air-bladder is developed as an outgrowth of the alimentary canal behind the gill region. The septa between the gill-sacs are narrowed so that these become mere slits and a gill-cover or operculum is developed from the hyoid. The nostril is divided into two openings, the eggs are small and the young emerge from them as larvae which undergo a long period of development before becoming adult.

Order I. **Teleostei.** Osteichthyes in which the notochord is surrounded and obliterated by bony amphicoelous centra developed from the connective bone outside the proper notochordal sheath. Between the centra the notochord persists. No intercalary arches are developed. The cartilage of the skull is covered by and largely replaced by bone and in particular a large median supra-occipital bone is always developed. The upper jaw is amphistylic articulating with the skull in front and supported by the hyoid behind. No splenial bone is developed in the lower jaw and there are no clavicles in the pectoral girdle. The tail is homocercal. The optic chiasma in the brain is resolved into two distinct nerves. The conus is amalgamated with the ventricle, and only one transverse row of pocket valves persists. There is no special valve in the intestine. The testis has a special duct opening by a special pore and in both sexes excretory ducts, genital ducts and alimentary canal open to the exterior by separate apertures.

Sub-order 1. **Clupeiformes.** Teleostei in which the pelvic fins are abdominal in position, the air-bladder has an open duct, the coracoid develops a mesocoracoid branch and in which there are no hard spines in the fin rays. The maxilla bears teeth and forms part of the gape.

Family 1. Clupeidae. Clupeiformes in which the oviduct is continuous with the ovary, air-bladder penetrates the skull and there are no adipose fins.

Ex. *Clupea, Engraulis.*

Family 2. Salmonidae. Clupeiformes with short oviducts with wide funnels, air-bladder normal. An adipose fin behind the dorsal.

Ex. *Salmo, Salvelinus, Coregonus,* etc.

Sub-order 2. **Anguilliformes.** Teleostei devoid of pelvic fins, and in which the pectoral girdle is disconnected from the skull. Air-bladder with open duct. No mesocoracoid and no hard spines in the fins. The premaxilla is lost, the maxilla if present bears teeth.

Ex. *Anguilla.*

Sub-order 3. **Ostariophysi.** Teleostei with abdominal pelvic fins and an open duct to the air-bladder. With a "Weberian chain" of ossicles connecting air-bladder and skull. A mesocoracoid is present.

Family 1. Cyprinidae. Ostariophysi in which the skin has normal thin cycloid scales. There is an interorbital septum and the symplectic is present. The maxilla does not bear a barbel.

Ex. *Cyprinus.*

Family 2. Siluridae. Ostariophysi in which the skin is naked or covered with ganoid scales beset with placoid denticles. The cranial cavity extends between the eyes, the symplectic bone is absent. The maxilla is toothless and carries a long barbel.

Ex. *Amiurus.*

Sub-order 4. **Haplomi.** Teleostei with abdominal pelvic fins and an open air duct to the bladder. No mesocoracoid and no Weberian chain.

Family. Esocidae. Supra-occipital separates the parietals. Ovaries and oviducts continuous with one another.

Ex. *Esox.*

Sub-order 5. **Percesoces.** Teleostei in which the pelvic fins are close behind the pectoral fins but not attached to the cleithra. The duct of the air-bladder is closed.

Family. Mugilidae. Percesoces in which the pelvic bones are attached to the postcleithra.

Ex. *Mugil.*

Sub-order 6. **Percomorphi.** Teleostei in which the pelvic bones are attached to the cleithra and in which the fins are consequently thoracic or jugular in position. The duct of the air-bladder is closed. Hard spines are developed in dorsal and anal fins and the skeleton of the pelvic fin usually consists of one spine and not more than five soft rays.

Family 1. Percidae. Percomorphi in which the dorsal fin is split into two fins, the front one alone having spines.

Ex. *Perca.*

Family 2. Centrarchidae. Percomorphi in which the dorsal fin is undivided.

Ex. *Micropterus.*

Family 3. Serranidae. Percomorphi in which the dorsal fin is undivided and in which a shelf supporting the eye-ball is developed from one of the circumorbital bones.

Ex. *Serranus.*

Family 4. Mullidae. Percomorphi with undivided dorsal fin and with a shelf for the eye-ball but with vestigial teeth and long gill rakers.

Ex. *Mullus.*

Family 5. Sparidae. Percomorphi with undivided dorsal fin and a shelf for the eye-ball; the teeth are large, cutting in front, crushing at the sides.

Family 6. Labridae. Percomorphi with undivided dorsal fin, no shelf for the eye-ball; the lower pharyngeal bones fused to form a single plate.

Family 7. Scombridae. Percomorphi with a few feeble spines in the dorsal fin and series of finlets behind the soft dorsal. The body is attenuated behind forming a stalk for the large caudal fin.

Ex. *Scomber*, *Thynnus.*

Sub-order 7. **Heterosomata.** Teleostei which habitually swim lying on one side in which both eyes are twisted on to the upper side of the head. Pelvic bones articulate with the cleithra, the air-bladder is lost. No hard spines are developed in the fins (except in one genus, *Psettodes*).

Ex. *Hippoglossus, Pleuronectes, Psetta, Psettodes, Solea.*

Sub-order 8. **Gadiformes.** Teleostei in which the pelvic fins are attached to the cleithra and are jugular in position, and in which the duct of the air-bladder is closed. No hard spines are developed in any of the fins and the primitive caudal fin is lost and replaced by a new caudal developed from portions of the anal and dorsal fins. A remnant of the cranial cavity persists above the interorbital septum in which the long stalks of the olfactory lobes lie.

Ex. *Gadus, Merlucius.*

Order II. **Aetheospondyli.** Osteichthyes in which the notochord is surrounded and entirely suppressed by the formation of opisthocoelous centra with well developed articulating surfaces. The articulating surfaces are developed out of dorsal and ventral intercalary cartilages which become ossified. No supra-occipital bone in the skull which is otherwise well ossified. The jaws are long and the maxilla represented by a series of bones. The upper jaw articulates with the skull behind the orbit but is still supported by hyomandibular and symplectic. Splenial and supra-angular bones in the lower jaw The tail fin a rounded lobe, the body is covered with ganoid scales beset with denticles forming fulcra on the anterior border of the tail fin. The conus is distinct in the heart and the optic chiasma in the brain. Ovary and oviduct are continuous and the testis discharges through the kidney by vasa efferentia. A spiral valve on the intestine. Air-bladder opens into pharynx in mid-dorsal line.

Ex. *Lepidosteus.*

Order III. **Protospondyli.** Osteichthyes in which dorsal and ventral intercalaries are present and join to form archless precentra at least in the tail region, the arch-bearing postcentra being formed from a ring connecting neural and haemal arch-pieces (basidorsals and basiventrals). Both pre- and postcentra are amphicoelous. No supra-occipital in the skull which is otherwise well ossified. The jaws are short, the maxilla is a single tooth-bearing bone. Splenial bone in lower jaw. A single gular plate on the under side of the throat. Tail fin a rounded lobe, body covered with thin cycloid scales. The conus distinct in the heart and the optic chiasma in the brain. Oviduct short, opening into coelom by a wide funnel. Testis discharging through the kidney by vasa efferentia. A spiral valve on the intestine. Air-bladder opens into pharynx in mid-dorsal line.

Ex. *Amia.*

Order IV. **Chondrostei.** Osteichthyes in which dorsal and ventral intercalaries are present as well as neural and haemal arches but in which no centra are found, the notochord being persistent and surrounded by an unsegmented cartilaginous tube. Few or no cartilage bones present in the cranium, jaws feeble and toothless connected to the skull only by hyoid. Numerous dermal bones on the head and the pectoral girdle. Clavicles present between the cleithra. Tail fin heterocercal with a row of fulcra on anterior lobe. Conus distinct in heart, optic chiasma in brain. Oviduct short and opening by a wide funnel into the coelom, testis discharging through kidney by vasa efferentia. Air-bladder opens into pharynx in the mid-dorsal line.

Family 1. Polyodontidae. Skin naked or with vestigial scales deeply embedded.

Ex. *Polyodon*, *Psephurus*.

Family 2. Acipenseridae. Skin covered with five longitudinal rows of bony scutes.

Ex. *Acipenser*, *Scaphirhynchus*.

Order V. **Polypterini.** Osteichthyes in which the notochord is surrounded and partly obliterated by amphicoelous bony centra resembling those of Teleostei. Both dorsal and ventral ribs present. Skull well ossified but devoid of supra-occipital bone. A splenial in the lower jaw and a pair of gular plates on the throat. Spiracle persistent and covered with a special cover formed from the postorbital bone. Clavicles present in pectoral girdle, pectoral fin with a median scaly lobe. The skin covered with ganoid scales beset with placoid denticles. A diphycercal tail fin. Conus distinct in heart and optic chiasma in brain. Oviduct short, opening by a wide funnel into coelom. Testis with special duct joining kidney duct near its external aperture. A spiral valve on intestine. Air-bladder bilobed and opening on ventral side of pharynx.

Ex. *Polypterus*, *Calamoichthys*.

Order VI. **Dipnoi.** Osteichthyes in which there are intercalary pieces but no centra, the notochord being surrounded by an unsegmented cartilaginous sheath. Few cartilage bones in skull, a median series of dermal roofing bones. The upper jaw fused with cranium, no premaxilla or maxilla. A diphycercal tail, body covered with thin cycloid scales, paired fins typically long and biseriate.

Conus distinct in heart with a spiral longitudinal valve, atrium divided into right and left auricles, an inferior vena cava present and pulmonary veins returning blood from air-bladder to heart. An optic chiasma in brain. Oviduct opens by a funnel into coelom. A spiral valve on intestine, air-bladder opens in mid-ventral line of pharynx.

Family 1. Monopneumona. Air-bladder undivided, young without external gills.

Ex. *Ceratodus.*

Family 2. Dipneumona. Air-bladder bilobed, young with external gills.

Ex. *Protopterus, Lepidosiren.*

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CHAPTER XXI

SUB-PHYLUM IV. CRANIATA

Division II. Gnathostomata

Sub-division I. Anamnia

Class II. Amphibia

Characters of the Class.

The class Amphibia includes the familiar Frogs and Toads, the less known Newts and Salamanders, and some very curious worm-like tropical forms which burrow in the earth. The name means double life (Gr. ἀμφί, double; βίος, manner of living), and refers to the fact that all the typical members of the class commence their lives as fish-like larvae, breathing by gills, and afterwards become converted into land animals, breathing by lungs. This strongly marked larval type of development is one of the great distinctions between the Amphibia and the only other class of Vertebrata with which they could be confounded, viz., the Reptiles. In the Reptiles, as in the Birds, a large egg abundantly provided with nutritive material is produced, and the young animal practically completes its development within the egg-shell and is born in a condition differing from the adult chiefly in size.

It might at first sight be thought that the fact that Amphibia breathe air in their later life and live on land would be sufficient to mark them off from the fish. But we have already seen that the older orders of Bony Fish use their air-bladders as lungs to assist in respiration, and on the other hand some Amphibia retain gills throughout life and rarely if ever leave the water.

The unbridged gap between true fish and Amphibia is to be found not in the breathing organ but in the structure of the limb. Fish possess fins—median and paired—which are in both cases supported by horny rays, as well as an internal skeleton; and the paired fins have an internal skeleton which has the form of a jointed axis bearing similar rays on one or both sides (Figs. 224 and 249).

The Amphibian limb, on the other hand, is what is known as a pentadactyle limb; that is to say, it is constructed on the familiar type of the human limb, and the median fin when present has no fin-rays (Figs. 251 and 253).

The pentadactyle or five-fingered limb (Gr. πέντε, five; δάκτῠλος, a finger), also called the cheiropterygium (Gr. χείρ, a hand; πτερύγιον, little wing, hence an appendage), consists of three segments, a proximal, containing one long bone; a middle, containing two bones placed side by side and occasionally fused into one; and a distal, containing a series of small squarish cartilages or bones arranged in lines so as to give rise to a series of diverging rays; the last-mentioned constitute the skeleton of the fingers and toes. In the proximal part of this lowest segment the bones are much crowded together and the rays tend to coalesce: this part has received a special name, as has also the portion where the rays although separate are embedded in the same muscular mass.

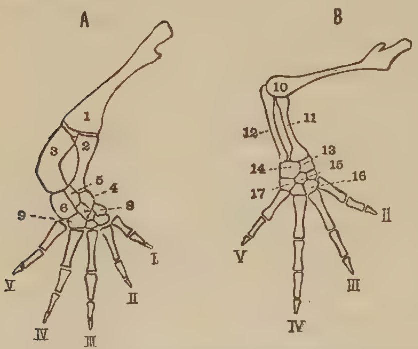

FIG. 251. A. Skeleton of a right posterior, B. skeleton of a right anterior limb of a Newt, *Molge cristata* × 1½.

1. Femur. 2. Tibia. 3. Fibula. 4. Tibiale. 5. Intermedium. 6. Fibulare. 7. Centrale of tarsus. 8. Tarsale 1. 9. Tarsalia 4 and 5 fused. I, II, III, IV, V. Digits. 10. Humerus. 11. Radius. 12. Ulna. 13. Radiale. 14. Intermedium and ulnare fused. 15. Centrale of carpus, the pointing line passes across carpale 2. 16. Carpale 3. 17. Carpale 5.

The fore-limb is called the arm, and its divisions the brachium or upper arm, the antebrachium or fore-arm, and the manus or hand (B, Fig. 251). The hind-limb is the leg, and its divisions are the femur or thigh, the crus or shank, and the pes or foot (A, Fig. 251).

The manus is divided into three regions, viz.: (*a*) the carpus or wrist where the rays tend to coalesce; (*b*) the metacarpus or palm where the rays although separate are bound together by flesh and skin · (*c*) the digits or free ends of the rays. The pes is similarly divided into tarsus or ankle, metatarsus or sole, and digits or toes.

The bone of the brachium is called the humerus, that of the femur bears the same name as the segment to which it belongs;

those of the antebrachium are called radius and ulna, those of the crus tibia and fibula (Fig. 251).

The skeletons of the pes and manus are typically exactly the same. Situated proximally close to the middle segment of the limb is a transverse row of three small bones, the central one being called the intermedium in both limbs, whilst the outer and inner are named after the bones of the middle segment of the limb adjacent to them. Thus we find in the wrist a radiale and ulnare and in the ankle a tibiale and fibulare. Distal to this row of bones there is a single central bone which probably belongs to the middle ray, and still more distally situated a row of five small bones corresponding to the digits. This last row are denominated carpalia in the wrist and tarsalia in the ankle. The individual bones are called carpale (or tarsale) 1—5 in accordance with the digits opposite which they are situated.

In almost every case this typical skeleton of nine bones has undergone some modification, owing either to the absence of some bones or the fusion of others, but in the hind-limb of the lower Amphibia it is exactly typical. In the higher Amphibia not only has great reduction of the elements taken place but the radius and ulna in the fore-limb and the tibia and fibula in the hind-limb have coalesced, a groove only being left to show their primitive distinctness.

The primitive position of the limbs with reference to the trunk is, from the study of development, assumed to be one in which they are stretched out at right angles to it, with the inner surface of the hand and the sole of the foot directed ventrally and in such a position that a line joining the tips of the fingers is parallel to the long axis of the body. If we suppose an imaginary line or axis to run down the centre of each limb, we shall be able to distinguish a pre-axial from a postaxial side. In the lower Amphibia the only change from this position that has taken place in the hind-limb is that each segment of the limb is bent at right angles on the one which follows it. The fore-limb is bent similarly, but it is also rotated backwards so that its upper segment is almost parallel to the axis of the body, and the elbow points backwards. If this position were maintained the first digit would become external; but the manus in most cases is at the same time twisted forwards so that the lower end of the radius lies internal to that of the ulna, and the radius thus crosses the ulna in its course. In the higher Vertebrata this twisting can be undone and the hand reverted to

an untwisted position. This movement is known as supination, the reverse movement being known as pronation.

FIG. 252. Skeleton of Triton, *Molge cristata* × 1.

The hind-limb in the higher Amphibia and other Vertebrata is likewise rotated forward so that the knee points forward and the first digit is internal, but this does not occur in the lower Amphibia, such as *Molge*.

The pectoral girdle is not essentially different in the lower Amphibia and the more primitive Osteichthyes, but the pelvic girdle is firmly joined to the transverse process of one of the vertebrae, which is called the sacral. This is one of the most distinctive features of all pentadactyle animals; it is a consequence of the adaptation of the pentadactyle limb to raise the body from the ground (Fig. 252). It is necessary for this purpose that the limb should have a firm purchase on the axial skeleton. Consequently when we find some Amphibia which never use their limbs for crawling but only for swimming, we assume that this is a secondary degenerate condition.

Next to the character of the limb one of the most distinctive features of Amphibia is the nature of the skin. Indeed the five great classes of Gnathostomata—Fishes, Amphibia, Reptiles, Birds, and Mammals—are each perfectly characterised by the nature of their skin. In a typical Amphibian the skin is soft and moist and devoid altogether of any ossifications like the scales of fishes. The skin is a most important breathing organ, since the lung alone cannot meet the demand for oxygen, and if the skin becomes dry and consequently incapable of absorbing oxygen the animal dies. The necessary moisture is supplied from a series of pockets, to form which the ectoderm is pouched inwards—or to use a more convenient term "invaginated"—at various points, and the cells lining these pouches have the power of secreting great quantities of mucus. As the cells become

broken up into mucus, new cells take their place, being budded off from the underlying Malpighian layer just as are the horny cells. These pouches are known as dermal glands.

The skull and brains are very characteristic, recalling in many points those of the Dipnoi. The axis of the brain appears straight, as in fishes; in higher Vertebrates this axis is more or less folded. In contrast, however, with fishes, the cerebral hemispheres of the fore-brain are relatively large, and, as in Dipnoi, have a roof consisting of nervous matter, whereas the cerebellum, usually so large in fishes, is reduced to a mere band (Fig. 263).

The skull always articulates by two pegs—the occipital condyles—with the first vertebra (Fig. 255). It is remarkable for its extremely flattened shape; the jaws are widely bent outwards so that the large eyes in no way compress the cranium, which is thus evenly cylindrical. Both membrane and cartilage bones are present, but the ossification is by no means complete. The exact arrangement of the bones will be given when a type is studied.

The vertebrae are either procoelous (Gr. πρό, in front; κοῖλος, hollow), or opisthocoelous (Gr. ὀπισθο-, behind), that is to say either concave in front and convex behind, or *vice versâ*, and the arrangement may differ in allied genera, while amphicoelous vertebrae also occur.

The vertebrae articulate with one another, not only by the centra but also by facets called zygapophyses (Gr. ζυγόν, a yoke), on the sides of the neural arches. The anterior facets, prezygapophyses, look upwards and are covered by the posterior facets or postzygapophyses of the vertebra in front, which look downwards.

The circulatory system closely resembles that of the Dipnoi. The atrium is divided into two auricles, and the blood from the lungs returns direct to the left auricle by the pulmonary veins. A median vein, the inferior cava, returns the blood from the kidneys directly into the sinus venosus, receiving in its course the hepatic vein. The anterior portions of the posterior cardinals are much reduced in size and may be altogether absent.

The lungs open by a common stem, the laryngeal chamber, into the throat. The opening is called the glottis, and its sides are stiffened with cartilage.

The kidneys and reproductive organs show essentially the same arrangement as in the Elasmobranchs, the kidney being divided into a sexual part connected with the testis and a posterior non-sexual part. There is one opening for all ejecta, the cloaca.

The ventral wall of the cloaca, however, is produced outwards into a great thin-walled sac, the allantoic bladder, in which when the cloaca is closed the urine accumulates. This organ acquires immense importance in the development of the higher animals and is found in no fish.

In the larva, which is to all intents and purposes a fish, there are present those peculiar sense-organs called mucous canals, supplied by the 5th and 10th nerves, but these are usually lost in the adult.

Classification.

Living Amphibia are divided into three well-marked orders, viz. the Urodela, the Anura and the Apoda. The Urodela (Gr. οὐρά, tail; δῆλος, conspicuous) have long cylindrical bodies and long flattened tails. The limbs are short and comparatively feeble, barely strong enough to lift the belly from the ground. Both pairs of limbs are about equal in size. The Anura (Gr. ἀν-, no; οὐρά, tail) have much broader and shorter bodies; the tail is totally lost and the hind limbs are powerfully developed and adapted for jumping. The Apoda (Gr. ἀ-, no, πούς, ποδός, a foot) have lost both pairs of limbs and their cylindrical bodies give them a worm-like appearance; their habits heighten the resemblance since they burrow in moist earth. They have embedded in the skin small bony plates, relics of the scales which their fish-like ancestors once possessed. The tail has in these animals almost disappeared.

In the Carboniferous rocks the remains of a large number of Amphibia have been found which have been called Stegocephala (Gr. στέγος, a roof; κεφἄλή, the head) from the circumstance that the head is covered with a compact mosaic of membrane-bones extending from the mid-dorsal line of the cranium outwards to the lips. Similar small bones or scales are found on the ventral surface. These features show resemblances to what is found in Dipnoan fish from which Amphibia are probably descended, and the small scales of the Apoda seem to be the last remnants of this armature. Stegocephala include both long and short tailed forms, and while some of their descendants—the Labyrinthodonta—became highly specialised in the structure of their teeth and died out in the next geological period, others, in all probability, gave rise to modern Amphibia.

Order I. **Urodela.**

Returning to the Urodela, which are the most primitive of modern Amphibia, we find that in Great Britain they are represented

by three species, all belonging to the genus *Molge* (*Triton*) and popularly known as Efts or Newts. *Molge cristata*, the Warty Eft, and *Molge vulgaris*, the Common Eft, are found in ponds and ditches all over the country, but *Molge palmata* is much more local. We may select *Molge cristata*, the Greater or Warty Eft, or Crested Newt, as a type of the anatomy of Urodela (Fig. 253).

The animal is about five or six inches long, half the length being made up of the tail, which has a continuous fringe of skin, the median fin. This fin in the male extends forwards to the head dorsally and is greatly enlarged in the breeding season, but it is at all times devoid of fin-rays.

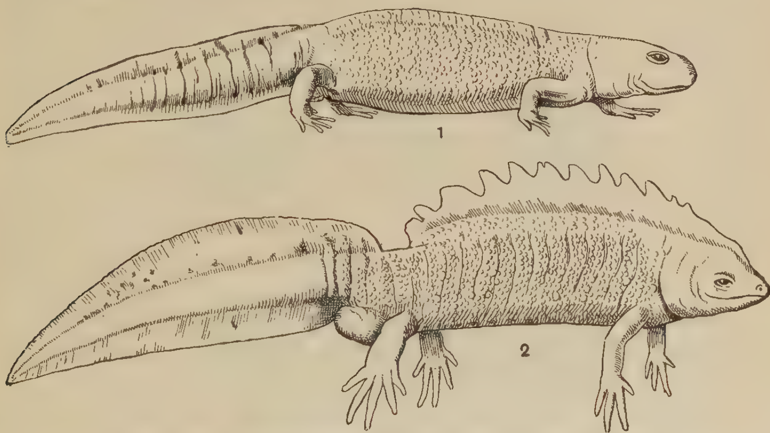

FIG. 253. *Molge cristata*, the Warty Eft. From Gadow.
1. Female. 2. Male at the breeding season with the frills well developed.

The skin is clammy, owing to the secretion of the dermal glands: it is dark coloured above and yellow spotted with black below. The opening of the cloaca is placed behind the hind-legs: it is a longitudinally placed oval slit which in the male has thickened lips.

The fore-limbs have only four fingers, the innermost corresponding to the human thumb being wanting, but there are five toes in the hind-limb. The animal when out of water crawls feebly along, but it swims actively in the water by means of its vertically flattened tail. The head is flattened dorso-ventrally and of somewhat oval outline, and the gape is of moderate extent. The eyes are small and project but little. The nostrils are very small and situated at the extreme front end of the snout.

If the newt be carefully watched when out of the water the skin of the underside of the head between the two sides of the lower

jaw will be seen to throb at regular intervals, being alternately puffed out and drawn in. It can be further seen that the nostrils are closed when the skin is drawn in and opened when it is puffed out. These movements constitute the mechanism of breathing in the newt. As in the case of the Dipnoi, the paired nasal sacs communicate with the interior of the mouth by openings called

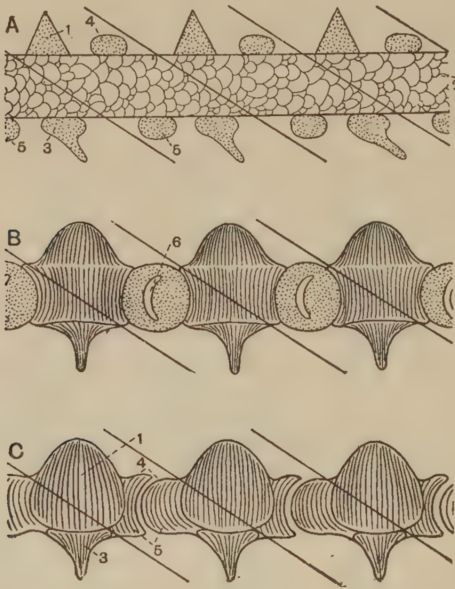

FIG. 254. Diagram illustrating three stages in the development of the vertebral column of an Opisthocoelous Urodela.

A. Stage in which basidorsals, basiventrals and intercalaries are separate.

B. Stage in which basidorsals and basiventrals have united with one another and in which the intercalaries have united to form an intervertebral pad of cartilage in which a synovial cavity is just appearing. This stage is permanent in some Urodela.

C. Stage in which the vertebrae are complete.

1. Basidorsal. 2. Notochord. 3. Basiventral. 4. Dorsal intercalary. 5. Ventral intercalary. 6. Synovial cavity. Dotting, cross-hatching, etc. as in Figs. 232 and 242.

the choanae or internal nares, and the air passes through these from the nostril when the cavity of the mouth is enlarged. When the cavity of the mouth is compressed the nostril is closed by a flap of skin constituting a valve, and the air is forced through the open glottis into the lung, whence it is forced out again by the elastic recoil when the pressure is removed.

If the animal be laid on a board with the ventral side uppermost and skinned, a thin sheet of muscles, the mylohyoid, will be seen stretching between the two halves of the lower jaw. When this muscle is relaxed the floor of the mouth is arched upwards and the underside of the head consequently becomes concave. When the muscle contracts and straightens, the cavity of the mouth enlarges and air is drawn in. Above the mylohyoid (underneath from the point of view of the dissection) are two longitudinal muscular bands, and in these are embedded the reduced remains of the visceral arches to which the gills of the larva were attached (Fig. 256). These muscles are called geniohyoid in front of the arches, sternohyoid between them and the pectoral girdle, and they are continued backwards along the belly as the straight muscles of the abdomen, the recti abdominis.

These sternohyoid muscles can draw the visceral arches downwards and backwards and probably assist the mylohyoid in depressing the floor of the mouth. The geniohyoid muscle on the contrary pulls the arches forwards and helps to restore them and the floor of the mouth with them to their old position. In this action muscles called petrohyoid, which run from the arches to the outer surface of the auditory capsule, also take part. These muscles are representatives of the levatores arcuum of fish (see p. 457), and they raise the arches and consequently the floor of the mouth.

The glottis or opening into the lungs is stiffened at the sides by a pair of cartilages, which it seems probable are the remains of a hinder pair of visceral arches: and these cartilages have muscles attached to their sides which drag them apart and which belong to the same series as those which raise the arches. Hence the same muscular action which lifts the floor of the mouth opens the glottis and admits air into the lungs.

How these muscles co-operate to effect the regular pumping of air in and out of the lungs has been thoroughly investigated only in the case of the Frog, and will be described when we come to deal with that animal.

The remaining muscles of the body are not much altered from those of the fish. In the tail and the ventral part of the trunk there are V-shaped myotomes, but this arrangement is disturbed in the neighbourhood of the limbs.

Skeleton.

Turning now to the skeleton we find that the vertebrae bear stout transverse processes with which are articulated short ribs (Fig. 252). The ribs borne by the sacral

vertebra are expanded in accordance with the strain put on them by the attachment of the ilium. Of the vertebrae those of the tail are the most primitive since they are composed of all the four pairs of arch-pieces; but of these only the basidorsals and the basiventrals become ossified at first, and joining together form the bulk of the vertebra, each basidorsal, as in fish, becoming connected with the basiventral belonging to the myotome in front, while the dorsal and ventral intercalaries, although likewise fusing together, remain cartilaginous and form the intervertebral cartilage. This either remains continuous and owing to its flexibility acts as a joint, or it becomes more or less separated into two portions which articulate with one another, one forming a cup and the other a ball. Joints in which the cup belongs to the posterior end of the vertebrae are called opisthocoelous, e.g., in *Desmognathus triton*, but the most frequent form of joint is one in which the ball forms the posterior and the cup the anterior portion of the vertebra. Such vertebrae are said to be procoelous. The portions of the intervertebral cartilage eventually become ossified and joined to the previously formed centrum. When the intervertebral cartilage does not form a joint but remains soft, the bony vertebrae in the dried skeleton appear to have the form of an hour-glass with cups at both sides—to be in fact amphicoelous, but they differ fundamentally from the amphicoelous vertebrae of Teleostei in that in these fish a portion of the notochord persists between two adjacent vertebrae, whereas in Urodela the notochord is obliterated between two successive vertebrae. The basiventrals of the tail vertebrae form long haemal arches.

In the trunk the basiventrals appear only in young larvae; in the adult they disappear so that the bulk of such vertebrae is formed only by the pair of basidorsals to which the ribs become secondarily attached by the formation of an outgrowth from the basidorsal termed the tubercular process (Fig. 254).

It is of importance to note that in many of the extinct Stegocephala, e.g., *Archegosaurus*, the caudal vertebrae were represented by four pairs of distinct arch-pieces, viz. basidorsals, basiventrals, and dorsal and ventral intercalaries, while the trunk vertebrae consisted of three separate pairs of pieces, namely the basidorsal, the dorsal intercalary, and the basiventral; but that in the typical Labyrinthodonts, the highest of the Stegocephala, all these constituent pieces were united into solid vertebrae; lastly, that in some of the lowest, e.g., in *Branchiosaurus*, each vertebra

consisted of a thin shell of bone surrounding the chorda, and composed of the basidorsals and basiventrals, which met each other, forming a broad-based section along the side of the vertebra, both partaking in the formation of a transverse process which carried the rib. It is of course possible and even probable that in these extinct forms dorsal and ventral intercalaries were present,

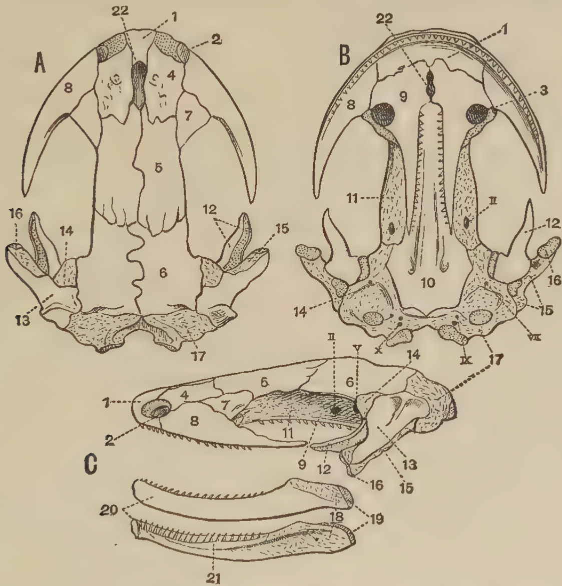

FIG. 255. A. dorsal, B. ventral, and C. lateral view of the skull of a Newt, *Molge cristata* × 2½. After Parker.

The cartilage is dotted, the cartilage bones are marked with dots and dashes, the membrane bones are left white.

1. Premaxilla. 2. Anterior nares. 3. Posterior nares. 4. Nasal. 5. Frontal. 6. Parietal. 7. Prefrontal. 8. Maxilla. 9. Fused vomer and palatine. 10. Parasphenoid. 11. Orbitosphenoid. 12. Pterygoid. 13. Squamosal. 14. Pro-otic region of fused exoccipital and pro-otic. 15. Quadrate. 16. Calcified cartilage forming the articular surface of the quadrate. 17. Exoccipital region of fused exoccipital and pro-otic. 18. Articular. 19. Articular cartilage. 20. Dentary. 21. Splenial. 22. Middle narial passage, a cleft in the cartilage of the snout filled with connective tissue. II, V, VII, IX, X. Foramina for the exit of cranial nerves.

forming intervertebral cartilages which were not ossified, for as we have just seen this state of affairs is found in some living Urodela. The haemal arches of the tail are, like the ribs, outgrowths of the basiventrals, but they do not exactly correspond to the ribs, for they are placed nearer the middle line.

In the skull the cranium is cylindrical, being quite uncompressed between the eyes. The bones of the jaws and face are widely arched outwards, so that the whole skull has a flattened shape. The nasal and auditory capsules form easily recognisable buttresses projecting from the cranium.

In both the floor and roof of the cartilaginous cranium the proper wall is largely deficient. The deficiency of the roof is the anterior fontanelle, that of the floor the greatly enlarged pituitary fossa. But these deficiencies are not seen in the uninjured skull, because the hole in the roof is closed in by two pairs of dermal bones, the frontals and the parietals, and that in the floor is underlaid by a broad parasphenoid dermal bone (Fig. 255).

Only at its extreme front and hind ends is the wall of the cranium converted into cartilage bone. In front there is on each side an orbitosphenoid bone, in the side wall, extending into the roof and floor and ossifying also the hinder wall of the nasal sac; behind, two exoccipital bones are placed at the sides of the foramen magnum, which they nearly encircle (Fig. 255). These bones bear the two condyles, so characteristic of Amphibia, for articulation with the vertebral column. There is no basi-occipital ossification, and in this point again Amphibia resemble Dipnoi.

The first visceral arch, which constitutes the cartilaginous jaws, is almost entirely cartilaginous. It consists of an upper part immovably attached to the skull, corresponding to the pterygoquadrate bar or upper jaw of Fish, and a lower part, Meckel's cartilage, forming the basis of the lower jaw. It will thus be seen that Amphibia resemble Holocephali and Dipnoi in this point. If we call this condition autostylic we do not do justice to the full extent of the resemblance between Dipnoi and Amphibia, for the jaw in the Notidanidae, which is movably articulated with the cranium, is also said to be autostylic. The name holostylic has been proposed for the condition of immovable junction between the cartilaginous upper jaw and the cranium, and this name we shall adopt. The same is true of all the higher groups of the Craniata. The upper jaw consists of two regions, the suspensorium which is fused with the skull and to which the lower jaw is attached, and the pterygoid process, a spur of cartilage which runs forward towards the nasal capsule. Both suspensorium and the articular end of Meckel's cartilage are slightly calcified. They are denominated quadrate and articular in Fig. 255, but there is no true bone present in either case. The front of the auditory capsule

is ossified by a large bone, the pro-otic, which in fully adult specimens becomes confluent with the exoccipital. The hinder visceral arches in the adult are present in a very degenerate condition. Traces of three remain (Fig. 256).

It is usual to speak of the hinder visceral arches of Amphibia and higher Vertebrata as the hyoid apparatus, or simply as the hyoid. The name suggests a misleading comparison with the second visceral arch of Fish; it is distinctly to be remembered that the hyoid bone of even Man contains more than this second arch; a good definition of the hyoid of Amphibia and higher animals would be "the degenerate remains of the hinder visceral arches."

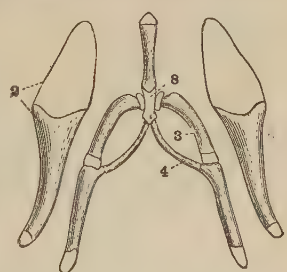

FIG. 256. Visceral arches of *Molge cristata*. The ossified parts are slightly shaded, the cartilage is white. From Parker.

2. Hyoid arch. 3. First branchial arch. 4. Second branchial arch. 8. Copula, i.e. the median piece connecting successive arches.

Turning now to the dermal bones of the skull, we find that it is roofed by three pairs, viz., the nasals, frontals and parietals. The nasals, of course, roof in the nasal sacs. In the palate there is one median bone, the parasphenoid, and three pairs of lateral bones, viz., the vomers in front of the posterior nares, the palatines fused with them and running along the edges of the parasphenoid, and lastly the pterygoids underlying the pterygoid process. Some of these bones are actually built up by the formation of a network of bone around the bases of minute conical teeth in the larva. The vomers and palatines retain their teeth in the adult, whilst the parasphenoid loses them, but in other genera of Urodela the parasphenoid may retain its teeth throughout life. When we were describing the skull of a Teleostean fish, bones named palatine and pterygoid (viz., ectopterygoid, entopterygoid and metapterygoid) were mentioned, but these were regarded as cartilage bones, i.e., as bones which arise in the connective tissue surrounding cartilage, and which subsequently eat into the cartilage, destroy it, and replace it.

Dermal bones, on the contrary, as the name implies, arise in the dermis or the connective tissue underlying the ectoderm. Now there is one situation where the dermis tends to become the "perichondrum," or connective tissue surrounding cartilage, and that is the stomodaeum or buccal cavity, whose lining membrane tends to be tightly stretched over the supporting visceral arches. Hence

bones originally dermal bones, like the pterygoid and palatine bones in Urodela, in more completely ossified animals, such as the Teleostei (and as we shall presently see in the higher Amphibia also), have begun to eat into the subjacent cartilage and thus to deserve the name of cartilage bones.

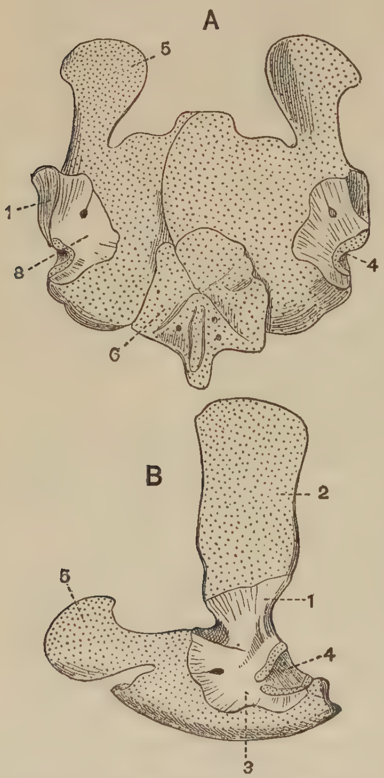

FIG. 257. A. ventral, and B. lateral view of the shoulder girdle and sternum of an old male Crested Newt, *Molge cristata* × 3. After Parker.

1. Scapula. 2. Suprascapula. 3. Coracoid. 4. Glenoid cavity. 5. Precoracoid. 6. Sternum.

The upper lip has tooth-bearing premaxillary and maxillary bones developed, the lower has a dentary on the outside of Meckel's cartilage and a splenial on the inner. Above the maxilla there is a small prefrontal bone.

If we examine the skeleton of the limbs we find that the pectoral girdle consists of two plates of cartilage which slightly overlap in the mid-ventral line. The lower half of each is forked, the forks being called precoracoid and coracoid respectively. The centre of each half of the girdle has a hollow termed the glenoid cavity for the articulation of the arm. All around the glenoid cavity the girdle is converted into bone; there is a bone termed the scapula above, and a coracoid bone below. The unossified part of the coracoid is simply termed the coracoid cartilage. The upper part of the girdle dorsal to the scapular bone is called the suprascapula. It remains cartilaginous, but is often calcified. The two coracoids are fastened behind to a small median cartilage called the sternum. The meaning of this will be discussed later.

The manus has only four fingers, the thumb and the corresponding small bone in the wrist or carpus having disappeared

and the ulnare and intermedium being fused, although they are distinct in the larva (Fig. 258, A). Otherwise the limb corresponds to the scheme given in the beginning of the chapter.

The pelvic girdle on each side is firmly joined to the rib of the sacral vertebra, and the two halves meet in the mid-ventral line. The upper part of the girdle above the cavity for articulation of the thigh is a bone, the **ilium**; below this cavity, which is termed the **acetabulum**, is a so-called "**ischio-pubic**" cartilage, in the hinder part of which a small bone, the **ischium**, is developed. In the mid-ventral line, in front of the union of the two halves of the pelvic girdle, there is a forked piece of cartilage, the **epipubis** (Fig. 259). In the pes the only departure from the typical arrangement is the fusion of the tarsalia 4 and 5.

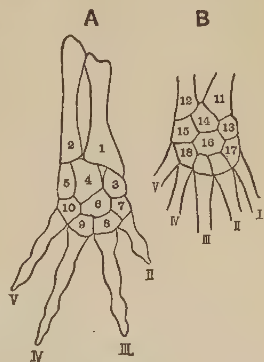

FIG. 258. A. Right antebrachium and manus of a larval Salamander, *Salamandra maculosa*. After Gegenbaur.

B. Right tarsus and adjoining bones of *Molge sp.* After Gegenbaur.

1. Radius. 2. Ulna. 3. Radiale. 4. Intermedium. 5. Ulnare. 6. Centrale. 7. Carpale 2. 8. Carpale 3. 9. Carpale 4. 10. Carpale 5. 11. Tibia. 12. Fibula. 13. Tibiale. 14. Intermedium. 15. Fibulare. 16. Centrale. 17. Tarsale 1. 18. Tarsalia 4 and 5 fused. I, II, III, IV, V. Digits.

Viscera.

If the muscles be carefully cut through in the middle line and reflected, the body cavity and the organs contained therein will be exposed. In general the difference from the arrangement of the organs in a Dog-fish is only in the relative size of the organs, in a word, in details.

The alimentary canal is thrown into a number of loops. The oesophagus is not in any way sharply marked off from the stomach, and the latter is nearly straight, extending only a short way round the bend of the first loop. There is a well-marked large intestine or **rectum**, ventral to which lies the bladder. The spleen is an oval red body lying at the side of the stomach and attached to the mesentery.

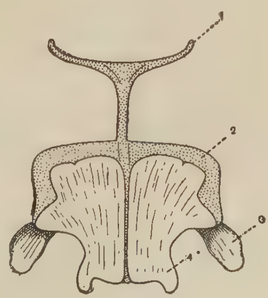

FIG. 259. Pelvic girdle of *Molge cristata* from below × 4.

1. Epipubis. 2. Ischiopubic cartilage. 3. Ilium. 4. Ischium.

The ducts of the pancreas and liver coalesce into a common stem before opening into the intestine.

The newt feeds on small worms and aquatic insects, which it

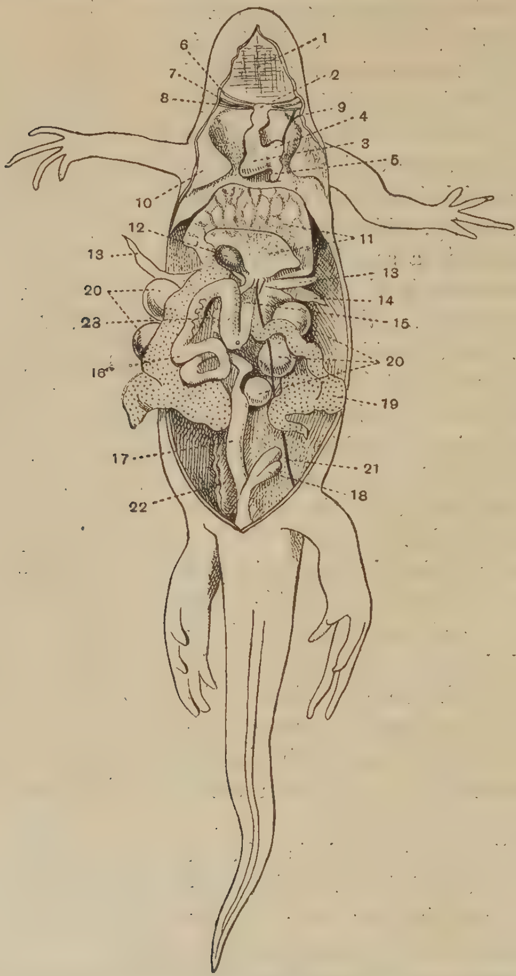

FIG. 260. A male *Molge cristata* cut open so as to expose the internal organs, about natural size.

1. Mylohyoid muscle with geniohyoid underneath. 2. Conus arteriosus. 3. Ventricle. 4. Auricle. 5. Sinus venosus. 6. Carotid arch. 7. Systemic arch. 8. Pulmonary artery. 9. Anterior vena cava of left side. 10. Coracoids pulled outwards. 11. Liver. 12. Gall-bladder. 13. Lung. 14. Spleen. 15. Stomach. 16. Intestine. 17. Rectum. 18. Allantoic bladder. 19. Fat-body. 20. Testes. 21. Anterior abdominal vein, displaced. 22. Kidney with duct. 23. Pancreas.

seizes with its jaws. Both upper and lower jaws are armed with minute teeth, and there are in addition two longitudinal rows of teeth on the roof of the mouth borne by the conjoined vomer and palatine on each side. The function of these teeth is not so much to crush as to retain a hold of the prey, which is swallowed whole. The tongue is a circular cushion on the floor of the mouth, supported by the second visceral arch. Its hinder edge is partially free. The lungs are long, smooth-walled, tube-like elastic sacs, attached to the liver and other organs at their base, but their tips float freely in the body-cavity.

Vascular System.

The heart lies far forward, between the roots of the lungs, enclosed in the pericardium. Externally all the four divisions of the piscine heart are visible, viz., sinus venosus, atrium, ventricle, conus. The venous system is essentially that of the Dog-fish, only the veins are indicated by names borrowed from human anatomy. Thus the blood from the head is returned by two internal jugular veins, representing the anterior cardinals of the fish. These are joined by external jugulars from the superficial part of the throat and face and by a subclavian vein from each arm. The common trunk formed by the union of all three is, of course, the ductus Cuvieri, but it is called the superior vena cava, and it receives on each side close to the middle line a posterior cardinal vein. As in fishes, this vein in its course breaks up into capillaries through the kidney; and along the outer edge of the kidney, its posterior portion, the renal portal, may be made out. The two renal portals when followed further back are found to coalesce in the caudal vein which returns the blood from the tail: each receives a sciatic vein from the dorsal side of the leg joined by a femoral from the ventral surface of the limb.

The increased importance of the hind-limb has brought with it this increase in the vessels draining it, which are represented only by the small pelvic vein in fishes.

There are certain vessels, however, unrepresented in any fishes except the Dipnoi. These are: first, the pulmonary veins, which receive the blood from the lungs and open directly into the left side of the atrium, which is separated from the rest by a septum and constitutes the left auricle; secondly, the inferior vena cava, a large trunk situated in the median dorsal line just beneath the aorta, which receives most of the blood that has traversed the kidneys and conveys it into the sinus venosus just between the

openings of the two superior venae cavae. The inferior cava coalesces with the hepatic veins returning blood from the liver: these thus lose their independent openings into the sinus venosus which they had in the Dog-fish. In its hindermost portion between the kidneys the vena cava joins the subcardinal veins, i.e. the collecting trunks formed by the blood which has percolated through the kidneys from the renal portal, and which open into the posterior cardinal veins in front.

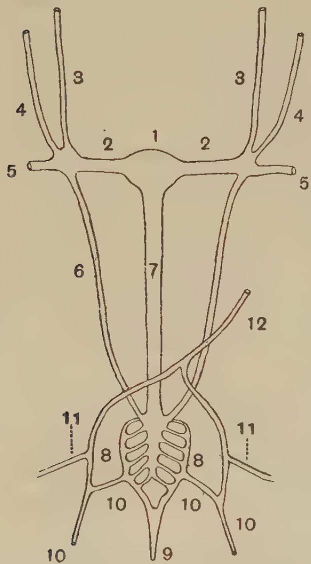

FIG. 261. Diagram to show arrangement of the principal veins of an Urodele.

1. Sinus venosus, gradually disappearing in the higher forms. 2. Ductus Cuvieri = superior vena cava. 3. Internal jugular = anterior cardinal sinus. 4. External jugular = sub-branchial. 5. Subclavian. 6. Posterior cardinal, front part. 7. Inferior vena cava. 8. Renal portal = hinder part of posterior cardinal. 9. Caudal. 10. Sciatic. 11. Femoral. 12. Anterior abdominal.

So far the peculiarities of the newt are shared by the Dipnoi: but there remain two veins highly characteristic of Amphibia. The musculocutaneous vein receives blood from the skin and pours it into the subclavian; we have already seen that the skin is a very important breathing organ, and this vein returns the blood which has been oxygenated in the skin to the heart. The anterior abdominal vein arises on the ventral side of the body near the cloaca from the union of two forks given off by the femoral veins; it runs forward in the mid-ventral line, eventually joining branches of the portal vein and entering the liver. This vein is found also in the lower Reptiles and in the embryos of Mammalia, where it is of the utmost importance in both nutrition and respiration; it has been compared to the lateral veins of Chondrichthyes (see p. 463) which are supposed to have become shifted inwards towards the mid-ventral line and to have partly coalesced.

When the veins are cut away it is possible to follow out the arteries. There is no ventral aorta, since on each side three arterial arches arise in a bunch from the front end of the tubular conus.

The first of these is called the carotid arch, and is derived from the third arterial arch of the embryo, but unlike its equivalent in Dipnoi it does not communicate with the dorsal aorta. It gives off a lingual artery to the tongue and throat and then passes up round the gullet, to which it gives off some twigs and continuing as the common carotid supplies the upper part of the head and brain. Just after giving off the lingual artery the arch swells up into a little knot, called the carotid gland. In this structure the channel of the artery is broken up into a network of fine passages and its function is believed to be that of holding back the blood from entering the head until, at the close of the contraction of the ventricle, the blood has returned from the lungs. The second arch, derived from the fourth embryonic arch, supplies most of the blood to the root of the dorsal aorta, and on this account is called the systemic arch. The fifth and sixth embryonic arches in later stages unite on each side into one trunk, which passing round the gullet joins the systemic arch (Fig. 262). The fifth arch disappears in *Molge*, as in all higher Vertebrates, but it is retained throughout life in the allied genus *Salamandra*. From the sixth arch is given off the pulmonary artery which supplies the lung. On this account it is called the pulmonary arch. The subclavian

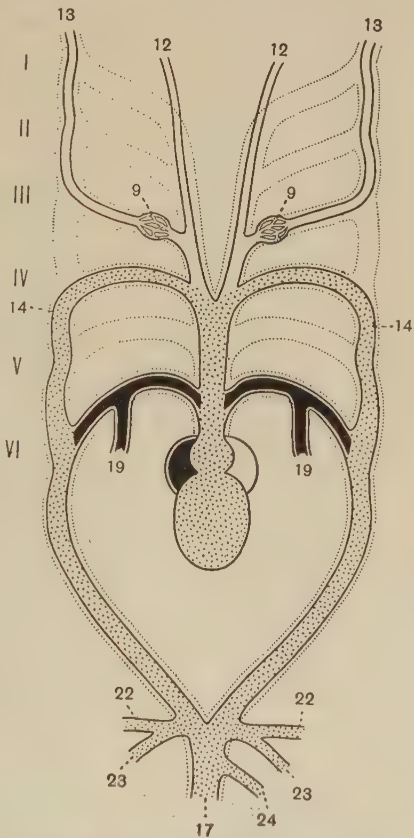

FIG. 262. Diagram of arterial arches of *Molge*, viewed from the ventral aspect.

I, II, III, IV, V, VI. First to sixth arterial arches. 9. Carotid gland. 12. Lingual (ventral carotid). 13. Common carotid (dorsal carotid). 14. Systemic arch. 17. Dorsal aorta. 19. Pulmonary. 22. Subclavian (dorsal type). 23. Cutaneous. 24. Coeliacomesenteric.

artery to the fore-limb on either side is given off just where the systemic arch unites with its fellows to form the dorsal aorta: hence it will be seen that this subclavian is of the dorsal type (p. 343). Each subclavian gives off a large branch to the other breathing organ, the skin, which is known as the cutaneous artery.

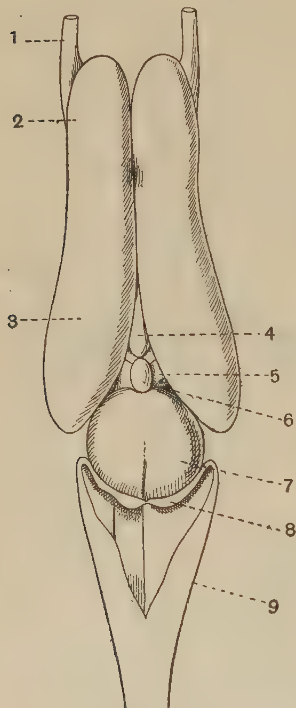

FIG. 263. Brain of Triton, *Molge cristata* × about 8.

1. Olfactory nerves, representing the olfactory lobes of the Dog-fish. 2. Olfactory lobes. 3. Cerebral hemisphere. 4. Thin roof of thalamencephalon. 5. Optic thalami. 6. Pineal body. 7. Mid-brain. 8. Cerebellum. 9. Medulla oblongata. From Burckhardt.

Nervous system.

It is comparatively easy to uncover the brain and spinal cord of the newt owing to the thinness of the bones which cover them. The cerebral hemispheres are long and cylindrical, and devoid of any other connection with one another than that by way of the thalamencephalon; through the thin roof of the latter two thickenings in its floor, the optic thalami, can be clearly seen. The mid-brain is a simple smooth vesicle, and the cerebellum is a slight inconspicuous transverse band (Fig. 263).

The olfactory lobe of Amphibia differs from that of Chondrichthyes and Gadiformes among Pisces in being separated from the cerebrum only by a slight constriction. From its anterior end a brush of nerve fibres is given off which goes to the nasal sac. These constitute the olfactory nerve. The stalk connecting the olfactory lobe and the cerebrum is unrepresented in the Amphibia.

The course of the cranial nerves is substantially the same as in the Dog-fish; owing, however, to the loss of the gills and the mucous canals in the adult, the branches are simplified. The 9th or glosso-pharyngeal, as its name implies, is distributed to the pharynx and tongue. The vagus supplies the larynx and glottis, but its main stem runs on to the heart and stomach.

The first spinal nerve comes out from behind the first vertebra and is called the hypoglossal; it runs directly to the respiratory muscle, the mylohyoid, crossing the vagus and glossopharyngeal in its course. At the sides of the dorsal aorta the two chains of sympathetic ganglia can be made out, connected by cross branches with the spinal nerves.

Urino-genital organs.

To turn now to the excretory system, the kidney can be seen when the alimentary canal is removed. It is a long narrow strip on each side adjacent to the aorta. In front it tapers to the merest thread, but behind, close to the cloaca, it thickens somewhat. Along its outer edge runs the archinephric duct, and external to the archinephric duct is situated the long oviduct.

The tubules which compose the kidney retain throughout life the ciliated openings into the body-cavity, and if the narrow part of the kidney be cut off and mounted in a little salt solution it is possible, at least in small specimens, under a low power of the microscope, to see the funnels and to observe the whirlpools due to the currents produced by their cilia.

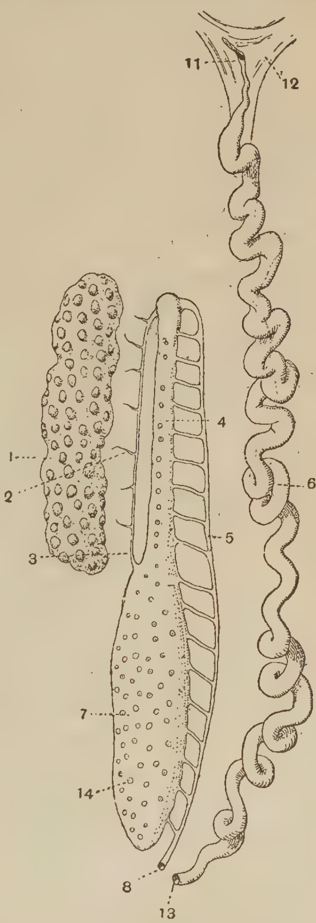

FIG. 261. Urino-genital organs of a female *Molge cristata* × about 5.

1. Ovary. 2. Remnant of vasa efferentia. 3. Remnant of longitudinal canal connecting the vasa efferentia. 4. Sexual portion of kidney. 5. Archinephric duct. 6. Oviduct. 7. Posterior non-sexual portion of kidney. 8. Opening of archinephric duct. 11. Internal opening of oviduct. 12. Suspensory ligament. 13. External opening of oviduct.

The genital gland in both sexes is represented by a pair of ridges suspended to the inner edges of the front parts of the kidney by slings of peritoneum similar to the mesentery suspending the gut, and on this account called mesenteries. In the female the oviduct opens

by a ciliated funnel adjoining the root of the lung. The funnel leads into a long convoluted tube running back to open into the cloaca. The testis, which takes the form of two conical bodies with their broad ends apposed, or sometimes a row of three rounded lobes, communicates by a number of vasa efferentia with the anterior part of the kidney, which is on this account termed the sexual portion or mesonephros. In the male the kidney tubules belonging to the hinder non-sexual portion, or metanephros, are split off from the archinephric duct and unite into a very short common trunk, the ureter, which joins the archinephric duct just before the latter enters the cloaca (Fig. 265).

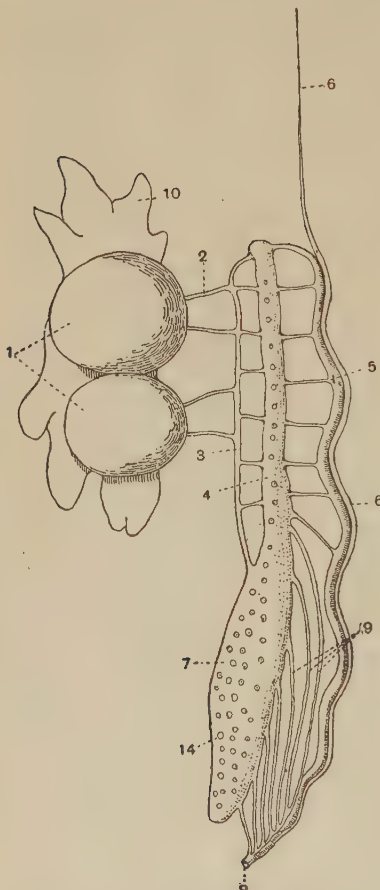

Fig. 265. Urino-genital organs of a male *Molge cristata* × about 5.

1. Testes. 2. Vasa efferentia. 3. Longitudinal canal connecting the vasa efferentia. 4. Sexual portion of kidney showing nephrostomes. 5. Wolffian duct. 6. Rudimentary oviduct. 7. Non-sexual portion of kidney. 8. External opening of the archinephric duct which has received the ureter 9 made up of a number of ducts from the posterior part of the kidney. 10. Fat-body.

It has been stated above that the genital glands are a pair of ridges. In the larva the inner portions of the ridges degenerate, the cells becoming largely converted into fat-bodies, i.e. lobes of peritoneum filled with connective tissue in which the cells secrete large drops of fat (stearate of glycerine) in their interiors and thus become swollen fat cells. In the adult these fat-bodies appear running parallel to the genital organs on the inner side. They serve as a store of nourishment for the eggs which develop during the winter-sleep. The newt, like other

Amphibia, passes the winter buried in the mud at the bottom of ponds and takes no food. The conversion of some of the possible eggs into fat to feed the rest is simply an example of the same principle as the sacrifice of some of the dogs in an Arctic expedition to feed the rest.

Larva.

The development of *Molge* is interesting. The male emits the spermatozoa in a bundle which the female then introduces into her cloaca, and the eggs commence their development in the body of the mother. Soon afterwards they are laid and attached to water plants. After some time larvae are hatched out which in many respects resemble fishes. They are provided with three long feathery appendages on each side of the neck, in which there is a rich blood supply and active circulation. These are the external gills found only in Amphibia, Dipnoi and in

FIG. 266. Larva of Triton, *Molge cristata* × 5. Showing external gills. After Rusconi.

Polypterus. There are also a pair of curious rod-like organs in front of the gills attached to the sides of the head. These "balancers," as they are termed, are possibly a first pair of external gills peculiarly modified. They have mucous cells at the tip, and by means of them the young larva suspends itself for hours at a time to plants. There is a long fish-like tail, the organ of locomotion, with a fringed fin. The fore-limbs are tiny buds. No trace of hind-limbs exists and the gill-slits are not open.

As development proceeds the fore-limbs make their appearance provided with only two toes. The gill-clefts, three in number, appear on each side. After a considerable time the third finger appears and the hind legs sprout out as buds; still later the fore-limbs get all four fingers and the hind-limbs five. The animal has now attained the appearance of the adult except in so far as the gills are concerned. These are retained for a long time, and exceptionally, in Switzerland in high Alpine localities, the larva may become sexually ripe and never leave the water. More usually with

the closing of the gill-slits and the shrivelling of the external gills the adult state is attained.

It has been recently pointed out that the development of the Newt's fore-limb may afford a hint as to how the pentadactyle limb was evolved from the fin of a fish. Prof. Broom has made the plausible suggestion that this took place by the gradual freeing of the anterior rays from the fin-membrane so that the limb was used for a time both to walk on and swim with, exactly as occurs in the pelvic fin of the modern gurnard (*Trigla*) where the anterior rays are freed from the membrane and are used by the fish to walk on the bottom. This freeing of the rays must have been a progressive process the fin-membrane shrinking as it was less and less used. The fingers of the Newt's hand appear one after the other and the oldest known foot-print of a land animal which is found in the Devonian rocks shows traces of only two well-developed toes.

Classification.

The Urodela have for a long time been divided into two main groups, according to the presence during adult life of gill-slits and gills. Huxley thus divided them into Ichthyoidea and Salamandroidea, and we shall adopt this mode of classifying Urodela although we fully admit that the group Ichthyoidea does not represent a single stem but probably several stems in the same condition. It is advisable to base classification on blood relationships when this is clear and undoubted, and this is possible in the case of the larger groups. But to follow out blood-relationship in minute detail is a very speculative matter in which the opinions of zoologists differ sharply, and if classification is to be continually altered in relation to such speculations no finality will be obtained and great inconvenience will result. Huxley's Ichthyoidea are those which retain throughout life gill-slits or external gills or both. Invariably the limbs are reduced in size, the animals rarely if ever leaving the water. In one case the hind-limbs have totally disappeared.

North America is the great head-quarters of the Ichthyoidea. *Menopoma* (*Cryptobranchus*) retains one gill-slit throughout life. This animal attains a length of 18 inches. It is fairly common on the Mississippi and its tributaries. An allied species found in Japan, and attaining a length of two feet, is the largest living Amphibian.

Amphiuma is a snake-like animal about 18 inches long, with one gill-slit. It is found in the same region as *Menopoma*. The limbs are exceedingly rudimentary, each having only two toes.

Necturus, the Mud-puppy, has small but well-developed limbs.

It retains throughout life two gill-slits and three external gills on each side. *Necturus* is abundant in the shallows of the St Lawrence, wriggling in and out around the roots of aquatic plants. A somewhat similar animal, *Proteus*, with more rudimentary limbs, is found inhabiting the limestone caverns of Carniola in Austria. Lastly, there is the aberrant *Siren*, which has a horny beak ensheathing the premaxilla and dentary; it has no hind-limbs, but is similar to *Necturus* in its gills: it is found inhabiting the swamps of the Southern United States.

Since the Ichthyoidea possess both gills and lungs it is at first sight tempting to regard them as the little modified descendants of an animal just making the transition from water-breathing to air-breathing life. There are however insuperable difficulties in the way of such an explanation. If we turn to other groups of the animal kingdom we find that the first step in fitting an animal for a land life is the covering up of the respiratory organ so as to protect it against drying up. But in hardly any fish are the respiratory organs so exposed as in *Necturus*, *Proteus* and *Siren*.

Further, it was pointed out that the great gap between fishes and Amphibia is to be found in the structure of the limb. But the Ichthyoidea do not in any way assist in bridging the gap. On the contrary their limbs are obviously degenerating, a fact which seems to show that the aquatic life has been re-acquired. Now when the similarity between say *Necturus* and the late larva of *Molge* is borne in mind, and the further fact that these larvae may abnormally become sexually ripe, the conclusion is irresistibly suggested that the Ichthyoidea are larvae in which the adult stage has been suppressed. In the case of one large American newt, *Amblystoma tigrinum*, the larva (the "Axolotl") often breeds under certain circumstances and was at one time regarded as a distinct genus (*Siredon*).

The second division of Urodela, the SALAMANDROIDEA, are in general very similar to *Molge*, both in appearance, anatomy and size.

As in Ichthyoidea, so likewise in Salamandroidea is North America very rich. These have been divided into families on grounds of differences in the skeleton which have little effect on the external appearance. The most abundant are the AMBLYSTOMATINAE represented by the genus *Amblystoma* of which there are many species, nine being found in the Eastern States and Canada. The members of this family are distinguished by having the palatine bones directed transversely, so that the vomeropalatine rows of teeth run across the roof of the mouth instead of along it, and by having

so-called amphicoelous vertebrae, i.e. vertebrae in which the intervertebral discs remain cartilaginous, not true amphicoelous vertebrae as in fish. *Molge* (*Diemyctilus*) *viridescens* is the common Waternewt of Lower Canada. It is a member of the same genus as the English Newt which has been selected for detailed description, but unlike its English congener the American species does not develop a crest in the breeding season. These Newts are representatives of the SALAMANDRINAE distinguished by having the vomeropalatine teeth in a longitudinal row and by possessing opisthocoelous vertebrae. The family DESMOGNATHINAE are closely allied to the Amblystomatinae, but differ from the latter in possessing a cluster of teeth on the parasphenoid in addition to the transverse row of vomeropalatine teeth and in having opisthocoelous vertebrae. The species of this family are common Water-newts in the Eastern United States. *Desmognathus nigra*, the Black Salamander, occurs near Montreal. The PLETHODONTINAE includes the American Cave- and Land-newts which rarely enter water but wriggle about actively on land. These Newts resemble the Desmognathinae in their teeth, but differ in possessing amphicoelous vertebrae. Although the most terrestrial in their habits of the New World Urodela, these animals and some of the Desmognathinae have undergone an extraordinary modification in their respiratory system. The lungs have disappeared and the septum between the auricles has become absorbed: so that the animals depend for their oxygen entirely on their skin and the lining of the pharynx, the walls of which still execute active respiratory movements. This curious association of terrestrial habits with the absence of lungs suggests the idea that the lung in such Urodela as retain it may be chiefly used as a hydrostatic organ like the air-bladder of fish, for were it of prime importance as a respiratory organ it would be difficult to explain its disappearance in terrestrial forms. *Spelerpes* includes the Cave-newts, of which there are twenty species in America and one isolated species in Italy. In these animals the tongue is long and not adherent to the floor of the mouth. It can be suddenly protruded and is used to catch insects in the same way as the tongue of the Anura. This is an exceptional action amongst Urodela, most of which seize their prey with the jaws. *Plethodon erythronotus* has the typical Urodele tongue. This is the common Land-newt in the neighbourhood of Montreal, being found under old logs and in other damp situations.

Order II. Anura.

The Anura or Batrachia are at once recognised by their broad, flattened, tailless bodies and their powerful hind-limbs. These limbs are not only efficient in jumping but also in swimming, and the toes are connected with one another by a thin web of skin in order to aid them in performing this function. The toes are stretched apart in the back stroke to present a large surface to the water, in the forward stroke they are folded together and offer little resistance.

Structure.

Anura are much more abundant than Urodela and are found all over the world, whereas the Urodela are restricted to the Northern hemisphere. They are in fact the dominant Amphibia of the present day, but they are highly specialised, and the Urodela give a much better idea of the relation of the Amphibia to the Fishes on the one hand and the Reptiles on the other, for which reason *Molge* was selected as the type.

Besides the absence of a tail, the powerful character of the hind-limbs and the differences in the skeleton connected therewith, Anura differ from Urodela in the skull and jaws, in the pectoral girdle, in the heart and lungs, and in the kidneys, genital organs and development.

Two genera and four species of Anura occur in the British Isles. *Rana temporaria*, the Common Frog, and *R. esculenta*, the Edible Frog, represent the Family Ranidae, but the latter of these two species is very possibly not indigenous but may have been introduced from the continent, while the Bufonidae or Toads are represented by *Bufo vulgaris*, the Common Toad, and by *B. calamita*, the Natterjack, which occurs in numbers in certain restricted localities, as a rule those with a sandy soil.

As the Common Frog, *Rana temporaria*, is easily attainable, the principal points in which it differs from *Molge* will be briefly described.

The Frog.

The animal when at rest normally squats on its haunches, supporting itself slightly on its palms. Under these circumstances, the pelvic girdle makes a considerable angle with the vertebral column and the powerful iliac bones raise the skin of the back into a well-marked hump, the so-called sacral prominence.

The gape is enormous, and is caused by the lower end of the suspensorium, or part of the skull to which the lower jaw is

hinged, slanting backwards instead of projecting directly downwards as in Urodela. The tongue is fixed to the floor of the mouth in front, but is free behind; it can be rapidly thrust out of the mouth by bending the posterior end forwards and it can be as rapidly retracted. It is used to whisk the insects on which the animal feeds into the mouth.

Behind the eye is a circular patch of thin, tightly stretched skin.

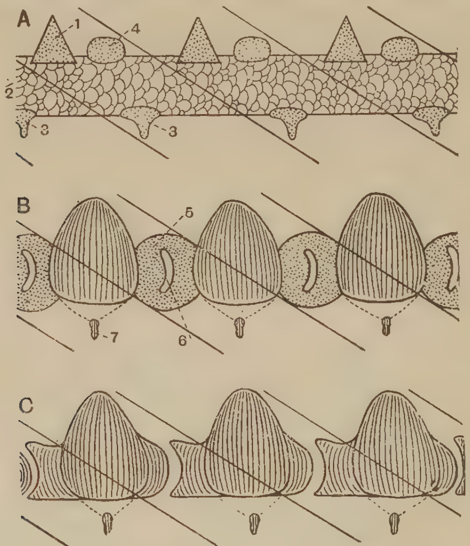

FIG. 267. Three diagrams illustrating the development of the procoelous vertebral column in Anura.

A. Stage in which basidorsals, basiventrals and intercalaries are separate.
B. Stage in which the basidorsals have extended downwards to form the main mass of the vertebra and in which the dorsal intercalary has formed an intervertebral cartilaginous pad in which a synovial cavity is appearing. The distal part of the basiventral has disappeared.
C. Stage of the completed vertebra.
1. Basidorsal. 2. Notochord. 3. Basiventral. 4. Dorsal intercalary. 5. Intervertebral pad. 6. Synovial cavity of cartilage. 7. Vestigial rib. Dotting, cross-hatching, etc., as in Figs. 232, 242 and 254.

This is the ear-drum or tympanic membrane, which closes externally the Eustachian pouch of the gullet. It is believed that this pouch or tympanum is the remains of the first gill-cleft, the spiracle of Elasmobranch fishes. Sound impinging on the ear-drum is conveyed to the wall of the ear capsule by a slender cartilaginous rod ensheathed in its middle part by bone, the so-called columella auris. In the Urodela sound has to find its way as best it can through the skin and muscle of the head to the auditory organ.

All Anura possess Eustachian pouches and a columella auris, but all do not have a well-developed ear-drum.

The skin is most loosely attached to the muscles underneath. Large spaces containing lymph are interposed between them. These lymph spaces form a protection against the danger of drying up. There are two pairs of sacs placed, one pair just between the upper ends of the pectoral girdle, and another pair just at the sides of the rudimentary stump of a tail, which have the power of contraction and pump the surplus lymph into the veins of the neighbourhood. These are called the anterior and posterior pairs of lymph-hearts.

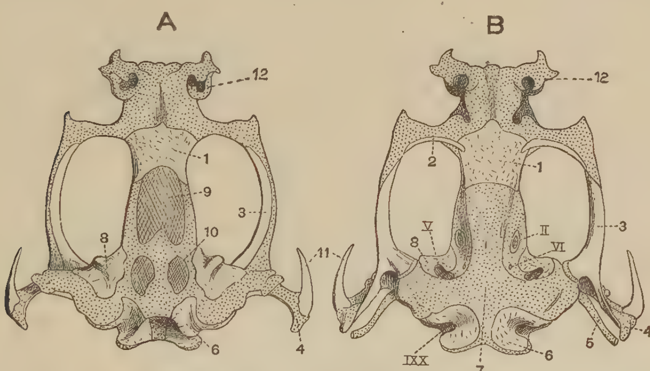

FIG. 268. A. dorsal, and B. ventral view of the cranium of a Common Frog, *Rana temporaria*, from which the membrane bones have mostly been removed × 2. After Parker.

1. Sphenethmoid. 2. Palatine. 3. Pterygoid. 4. Suspensorium. 5. Columella. 6. Exoccipital. 7. Ventral cartilaginous wall of cranium. 8. Pro-otic. 9. Anterior fontanelle. 10. Right posterior fontanelle. 11. Quadratojugal. 12. Nasal capsule. II, V, VI, IX, X. Foramina for exit of cranial nerves.

Turning now to the skeleton we observe many points of difference between the frog and the Newt. The ribs in the frog are indistinguishably fused with the transverse processes; in very few Anura are they distinct and they are always vestigial. The vertebrae differ from those of the Urodela in the entire suppression of the ventral intercalary element, so that the centrum is constructed out of basidorsal, interdorsal and basiventral elements, the last named being vestigial. In some Anura the basiventral piece is entirely absent, and in this case, since the centrum is constructed entirely of dorsal elements, the notochord is found for a considerable period of development lying in a groove on its under surface. This

is the so-called epichordal type of development. The tail vertebrae are represented by a bony style, the urostyle. Besides it there are only nine vertebrae. The transverse processes, or "diapophyses" of the ninth or sacral vertebra, to which is attached the ilium, are either cylindrical as in *Rana*, or they are more or less wide and flat as is the case in *Bufo* and *Hyla*. The diapophysis does not, like the so-called parapophysis of Teleostei, represent the proximal portion of the rib but is a secondary outgrowth of the neural arch-piece or basidorsal and the rudimentary rib is represented by a nodule

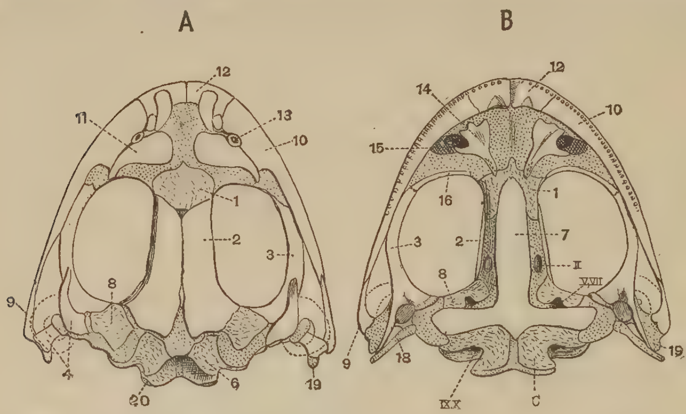

FIG. 269. A. Dorsal view of the skull of a Common Frog (*Rana temporaria*) × 2. B. Ventral view of the same. Both figures after Parker.

In this and in Figs. 270 and 272 the cartilage is dotted, cartilage bones are marked with dashes, membrane bones are left white.

1. Sphenethmoid. 2. Frontoparietal. 3. Pterygoid. 4. Squamosal. 6. Exoccipital. 7. Parasphenoid. 8. Pro-otic. 9. Quadratojugal. 10. Maxilla. 11. Nasal. 12. Premaxilla. 13. Anterior nares. 14. Vomer. 15. Posterior nares. 16. Palatine. 18. Columella. 19. Quadrate. 20. Occipital condyle. II. Optic foramen. V, VII. Foramen for exit of trigeminal and facial nerves. IX, X. Foramen for exit of glossopharyngeal and pneumogastric nerves.

attached to the distal end of this diapophysis, which may either fuse with the diapophysis as in *Rana* or remain distinguishable throughout life as in *Alytes* (Fig. 267).

The skull is constructed on the same plan as that of *Molge*, but it is broader and flatter; this is due to the wide arching out of the upper jaws, leaving a very large opening between them and the cranium. The cause of this again is to be sought in the large protruding prominent eyes, so marked a feature of all Anura. The floor of the cartilaginous cranium is complete in the frog, the pituitary fossa having sunk to insignificant dimensions. The orbitosphenoids have coalesced to form a box-like bone which ossifies

not only in the front part of the cranium but also in the hinder parts of the nasal sac, and is called the sphenethmoid. The parietal is fused with the frontal.

The suspensorium sends forward a pterygoid process which becomes attached to the skull in the nasal region. Underneath the posterior part of the pterygoid process there is a pterygoid bone which surrounds it and partly replaces it. The pterygoid sends out a fork which underlies that part of the suspensorium which forms an articulation for the lower jaw. The front part of the pterygoid process where it bends in to rejoin the skull is ossified by the palatine, which like the pterygoid has become a cartilage bone. The palatine is transverse to the axis of the skull, as in *Amblystoma*. Neither palatine nor pterygoid bears teeth, but the vomers bear a little group of teeth towards their hinder edge. These vomerine teeth are used for crushing the food, and are present in species like the Toad where the teeth borne by premaxillae and maxillae have been lost.

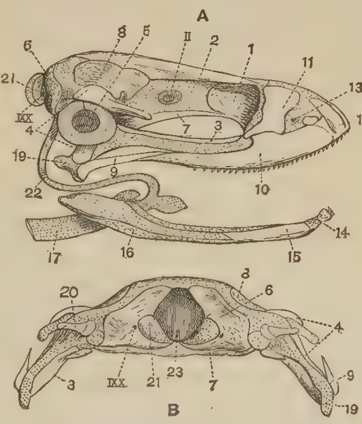

FIG. 270. A. Lateral view of the skull of a Common Frog, *Rana temporaria* × 2. B. Posterior view of the skull of the same. Both figures after Parker.

1. Sphenethmoid. 2. Frontoparietal. 3. Pterygoid. 4. Squamosal. 5. Tympanic membrane. 6. Exoccipital. 7. Parasphenoid. 8. Pro-otic. 9. Quadratojugal. 10. Maxilla. 11. Nasal. 12. Premaxilla. 13. Anterior nares. 14. Predentary. 15. Dentary. 16. Splenial. 17. Basilingual plate. 19. Quadrate. 20. Columella. 21. Occipital condyle. 22. Anterior cornu of the hyoid (ceratohyal). 23. Foramen magnum. II, IX, X. Foramina for the exit of cranial nerves.

The upper lip has a series of three bones on each side, reaching completely to the suspensorium, an additional quadratojugal being added to the two present in the Newt. The presence of this bone suggests that the ancestors of the Anura are to be sought amongst that highly modified group of the Stegocephala termed the Labyrinthodonta. In them as in the Anura the ventral inter-calary element was absent but at any rate in the earlier forms the basidorsals, the basiventrals and the interdorsals were distinct pieces. In all Anura there is a large membrane bone of a characteristic T-shape, known as the squamosal, lying outside the suspensorium. In the lower lip there is a splenial and a dentary, whilst in front the cartilaginous lower jaw is replaced by a pre-

dentary bone. In the frog only the premaxilla and maxilla and vomer bear teeth. Most Anura agree with the Frogs in this, but, as already mentioned, the Toad, *Bufo*, and its allies are entirely toothless (Figs. 269, 270).

The hinder visceral arches are reduced to a still more rudimentary condition than those of *Molge*. They are represented by a thin plate of cartilage called the basilingual with short blunt processes, of which only the last pair, which embrace the glottis, are ossified (Fig. 271). This pair are termed the thyrohyals. The whole "hyoid" is thus the remains of the visceral arches.

The pectoral girdle is much more strongly developed than in the Urodela. The coracoid and precoracoid processes are joined at their inner ends by a longitudinal bar, the epicoracoid, so as to enclose a space called the coracoid foramen. The two epicoracoids

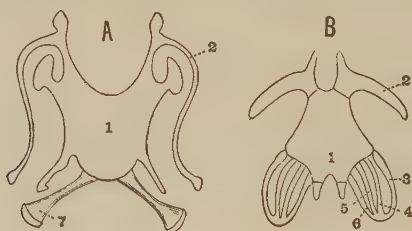

FIG. 271. Visceral arches of Amphibia. A. *Rana temporaria* adult. After Parker. B. Tadpole of *Rana*. After Martin St Ange.

In A the ossified portions are slightly shaded, while the cartilaginous portions are left white.

1. Basilingual plate. 2. Hyoid arch. 3. First branchial arch. 4. Second branchial arch. 5. Third branchial arch. 6. Fourth branchial arch. 7. Thyrohyal = fourth branchial arch.

are in the frog firmly united in the middle line. In many Anura however they merely overlap (Fig. 272, B).

The upper portion of the pectoral girdle is ossified by a bone called the scapula. As in Urodela, however, the cartilage projects a long way beyond it, and this portion is called the suprascapula and may become partially ossified. There is a distinct coracoid bone ossifying the coracoid process, and the precoracoid is underlain by a dermal bone called the clavicle. In front of the pectoral girdle in the middle line lies a small rounded piece of cartilage called the episternum, followed by a bony piece, the omosternum. Behind the girdle in a similar position is a cartilaginous bar with a flattened end, ensheathed by a bone called the sternum; the flattened end is called the xiphisternum. The omosternum has

proved to be composed of a portion budded off by the conjoined epicoracoids. The sternum is supposed to be the first sign of the breast-bone of higher Vertebrates, and it is almost certainly formed as a piece budded off from the conjoined epicoracoids behind.

In the arm the two points to be noticed are the complete fusion of the radius and ulna into one bone, and the reduction of the carpus, in which there are only six bones, three of the distal small bones having coalesced and the centrale being absent. The first digit or pollex is rudimentary.

In the pelvic girdle there is no epipubis: the ilium is a very long cylindrical bone: the ischium ossifies most of the ischiopubic

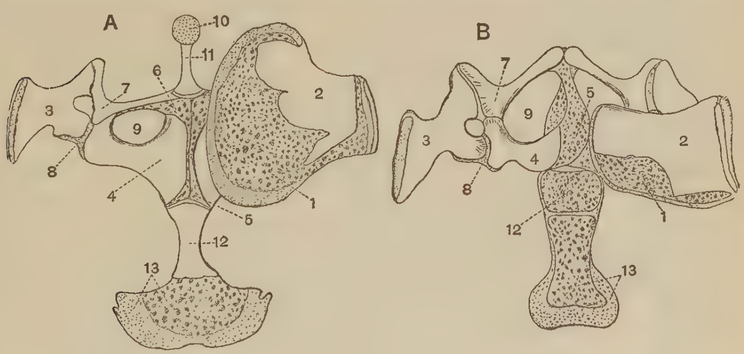

Fig. 272. Shoulder-girdle and sternum of

A. An old male Common Frog, *Rana temporaria*.

B. An adult female Toad, *Docidophryne gigantea*. To illustrate the difference in structure between Firmisternia and Arcifera. Both figures after Parker.

In both A and B the left suprascapula is removed. The parts unshaded are ossified; those marked with small dots consist of hyaline cartilage, those marked with large dots of calcified cartilage.

1. Calcified cartilage of suprascapula. 2. Ossified portion of suprascapula. 3. Scapula. 4. Coracoid. 5. Epicoracoid. 6. Precoracoid. 7. Clavicle. 8. Glenoid cavity. 9. Coracoid foramen. 10. Episternum. 11. Omosternum. 12. Sternum. 13. Xiphisternum.

cartilage and is closely applied to its fellow. In the leg the tibia and fibula are fused into one bone, which is about the same length as the femur. The ankle is remarkably elongated, the tibiale and the fibiale being long cylindrical bones, easily mistaken for the middle segment of the limb. The distal bones of the tarsus have nearly disappeared, only two or three small nodules being present on the axial side. The longest toe is the fourth, that corresponding to the human big toe (hallux) is the shortest. It is a matter of great interest to see on the inner side of the foot a spur supported by a small bone which may be the vestige of a sixth

digit. It is a common occurrence for the number five to be diminished, but very rare for it to be increased, but if the pentadactyle limb was derived from a fin like that of the Dipnoi by a shortening of the main axis and a reduction in the number of rays, it would be not unnatural to expect to find in the lower groups of land animals traces of extra rays.

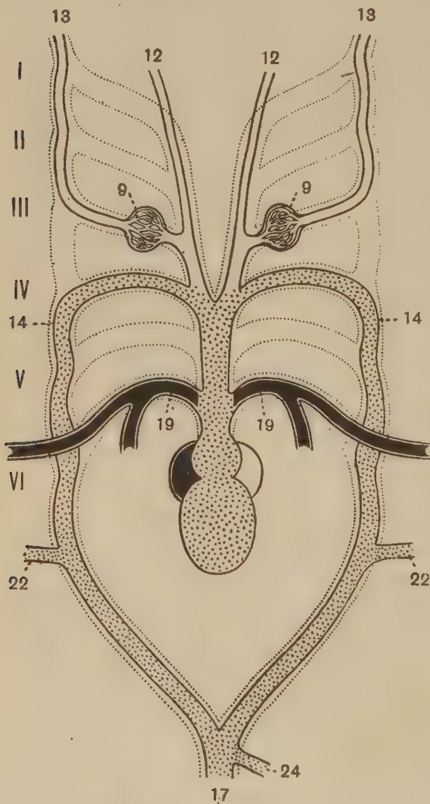

Fig. 273. Diagram of arterial arches of Frog viewed from the ventral aspect.

I, II, III, IV, V, VI. First to sixth arterial arches. 9. Carotid gland. 12. Lingual (ventral carotid). 13. Common carotid (dorsal carotid). 14. Systemic arch. 17. Dorsal aorta. 19. Pulmocutaneous artery. 22. Subclavian (dorsal type). 24. Coeliacomesenteric.

The main differences between the circulatory system of the frog and that of the Newt are to be found in the arterial system. Not only as in the Newt does the fifth arterial arch of the embryo disappear altogether, but the sixth becomes entirely cut off from the aorta and in addition to supplying the lung it sends a large branch to the skin, for which reason it is called the pulmocutaneous arch (Fig. 273). The conus arteriosus, as in *Molge*, has two transverse rows of pocket valves, one near the heart and one near the outer end, but in the frog there is in addition a longitudinal valve with a free ventral edge running somewhat obliquely from the one row of valves to the other. When the ventricle contracts, the blood from the right and left auricles lies on opposite sides of its cavity, and this cavity is converted into a series of ramifying passages by the numerous muscular trabeculae traversing

it, so that the two kinds of blood do not mix in it to any great extent. The opening of the conus is on the right side of the heart (left side as seen from below, Fig. 274), and at the beginning of contraction the venous blood on the right side of the ventricle flows into the conus. At this stage the conus is relaxed, a condition which arranges the longitudinal valve in such a way as to divert the blood almost exclusively into the pulmonary passages,

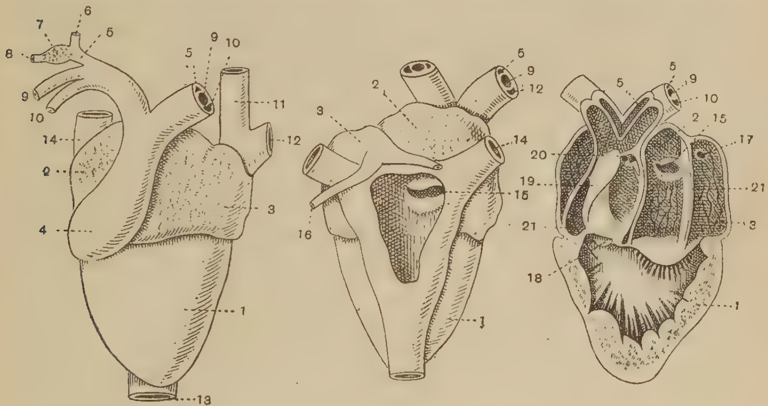

FIG. 274.

A. The heart, after removal from the body, seen from the front, the aortic arches of the left side having been removed. From Howes.

B. The same from behind, the sinus venosus having been opened up, to show the sinu-auricular valves.

C. The same, dissected from the front, the ventral wall together with one of the auriculoventricular valves having been removed.

1. Ventricle. 2. Right auricle. 3. Left auricle. 4. Truncus arteriosus. 5. Carotid arch. 6. Lingual artery. 7. Carotid gland. 8. Carotid artery. 9. Systemic arch. 10. Pulmocutaneous arch. 11. Innominate vein. 12. Subclavian vein. 13. Vena cava inferior. 14. Vena cava superior. 15. Opening of sinus venosus into right auricle. 16. Pulmonary vein. 17. Aperture of entry of pulmonary vein. 18. Semilunar valves. 19. Longitudinal valve. 20. Point of origin of pulmocutaneous arch. 21. Rod passed from ventricle into the truncus arteriosus, indicating the course taken by blood which flows into the carotid and aortic arches.

whose width and shortness also favours its flow into them. As these become filled the conus contracts, and this has the effect of making the longitudinal valve lie against the openings into the pulmonary arches and so preventing any more blood entering them, while at the same time the path into the systemic arches is widely opened. By this time some of the purified blood received from

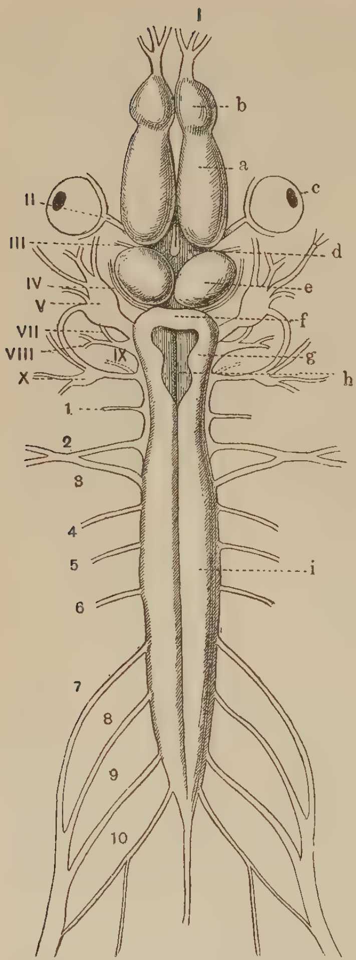

FIG. 275. Brain and spinal cord of a generalised Anuran. In the Phaneroglossa the 1st spinal nerve is suppressed. × about 2.

a. Cerebral hemisphere. b. Olfactory lobe. c. Eye. d. Thalamencephalon. e. Optic lobes. f. Cerebellum. g. Medulla oblongata. h. Fourth ventricle. i. Spinal cord. I. Olfactory nerves. II. Optic nerve. III. Oculomotor nerve. IV. Pathеticus. V. Fifth nerve. VII. Facial nerve. VIII. Auditory nerve. IX. Glossopharyngeal nerve. X. Vagus nerve. 1—10. First to tenth spinal nerves. 2 and 3 unite to form the brachial, and 7, 8, 9 and 10, to form the sciatic plexus.

the left auricle has been driven over to the opening of the conus from the left side of the ventricle, and so mixed blood passes to the hinder portion of the body. When the pressure in the ventricle rises to its highest point, the last blood, which is almost completely arterial,—all from the right auricle having been driven out,—is able to overcome the resistance in the carotid gland and go to the head, which contains the organs having the greatest need for thoroughly oxygenated blood.

The posterior cardinal veins are represented only by their hinder portions, the renal portals, all the blood from the kidneys being carried to the heart by the inferior vena cava.

The brain of the Frog and of Anura in general is more highly developed than that of the Urodela. Thus (Fig. 275) the olfactory lobes of the cerebral hemispheres are connected together, and the optic lobes of the mid-brain are well developed.

It was pointed out (p. 452) that the limbs of Vertebrates are in all probability derived from two lateral flaps of skin, that is, two longitudinal fins. The muscles in these fins were originally prolongations of the myotomes, and the nerves were of course branches of the

motor nerves going to the myotomes. Now as these longitudinal flaps were converted into paired fins, and these by a continual narrowing of their bases acquired greater distinctness from the body, the portions of the myotomes supplying the musculature and the nerves in connection therewith became so to speak bunched together at the base of the limb. In adult Craniata all trace of the original metameric arrangement of the limb muscles is lost; but the metamerism of the nerves can still be seen, and the bundles of these supplying the pectoral and the pelvic limbs are known as the brachial and the sciatic plexus respectively. In the frog, where the limbs are of far greater importance to the life of the animal than are the fins to fish, the nerves forming the brachial and the sciatic plexus are powerful trunks (Fig. 275, 2, 3, and 7—10).

The lungs are shorter than in the Newt but much wider, and their inner surface is covered with a network of low ridges which much increases their area.

The breathing movements of the frog have been analysed in detail, and we may give the results of this analysis as an example of respiratory movements in general amongst Amphibia, for there is little doubt that all Amphibia breathe in much the same fashion. The breathing movements of the frog have been classified into (*a*) aspiration, (*b*) expiration, (*c*) inspiration.

In aspiration air is drawn into the buccal cavity through the nostrils, this cavity being enlarged (as described in the case of the Newt) by the contraction of the mylohyoid muscle. In expiration air is forced out of the lungs into the buccal cavity and mingles here with the pure air drawn in from outside. This is effected by the dragging apart of the arytenoid cartilages guarding the opening of the glottis whilst at the same time pressure is put on the lungs by the contraction of the sternohyoid muscle which drags back the basilingual plate towards the pectoral girdle. Finally in inspiration the mixed air is pumped back into the lungs.

The pressure on the lungs is relieved by the contraction of the geniohyoid muscle which drags the basilingual plate forwards and the buccal cavity is reduced in size by the elevation of the basilingual by the action of the petroglossal muscles which attach it to the skull.

In the last phase of this movement some air must escape through the nostrils otherwise the frog would be continually taking in air and giving out none, which is an impossibility.

The kidney is a comparatively short and broad organ, very different from the long tapering organ of the Newt. The testis is connected by vasa efferentia with certain special tubules of the kidney. These tubules do not open into the archinephric duct, but into a special duct which runs along the surface of the kidney and

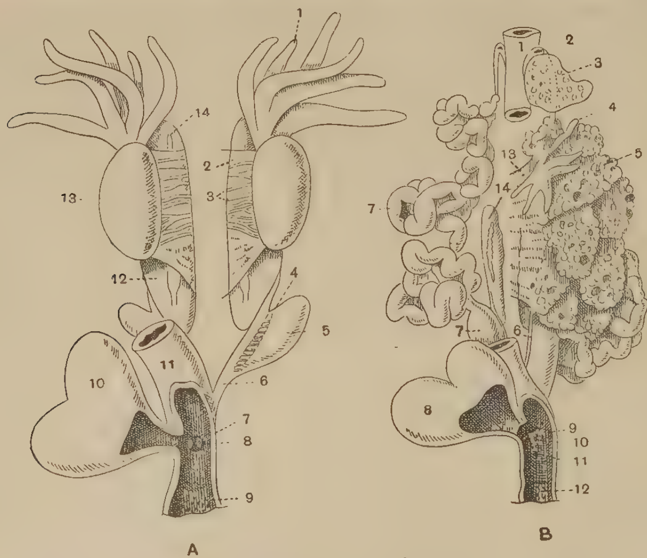

FIG. 276. The Frog.

A. The urino-genital organs of the male, dissected from the front, after removal from the body. From Howes.

B. The urino-genital organs of the female, dealt with in the same manner as the above, except that, in order to show the natural relations of the mouth of the oviduct, the left lung and a portion of the oesophagus were also removed from the body.

A. 1. Fat-body. 2. Fold of peritoneum supporting the testis. 3. Efferent ducts of testis. 4. Ducts of vesicula seminalis. 5. Vesicula seminalis. 6. Archinephric duct. 7. Cloaca. 8. Orifice of ureter. 9. Proctodaeum. 10. Allantoic bladder. 11. Rectum. 12. Kidney. 13. Testis. 14. Adrenal body.

B. 1. Oesophagus. 2. Mouth of oviduct. 3. Left lung. 4. Corpus adiposum. 5. Left ovary. 6. Archinephric duct. 7. Oviduct. 8. Allantoic bladder. 9. Cloaca. 10. Aperture of oviduct. 11. Aperture of archinephric duct. 12. Proctodaeum. 13. Fold of peritoneum supporting the ovary. 14. Kidney.

opens into the archinephric behind. Thus in a somewhat different way the separation of urine and spermatozoa is carried out quite as efficiently as in the Newt. The archinephric duct has a number of pouches developed on its walls which collectively form the vesicula seminalis in which the spermatozoa are stored up. In

Bombinator the vasa efferentia apparently open directly into the archinephric duct in front of the kidney. These vasa efferentia, like those of *Lepidosiren* (see p. 508) must be regarded as modifications of a conjoined vas efferens and kidney tubule which constituted the original connection between testis and kidney.

Lying on the ventral surface of the kidney near its inner edge is an elongated body called the adrenal body (14, Fig. 276, A). This organ is found under various forms in most Vertebrates; it has been recently shown to be derived from a peritoneal furrow which becomes shut off from the general coelom and loses its cavity, forming a solid rod of cells. Experiments made on higher animals and the observation of cases where it is attacked by disease, show that the adrenal bodies, like the thyroid, produce an "internal

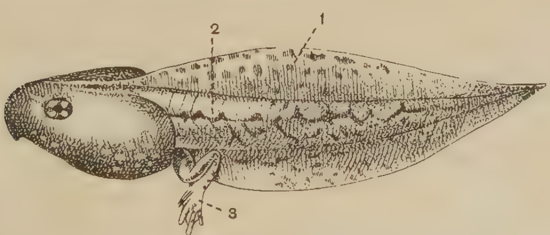

FIG. 277. Tadpole of *Rana esculenta*, Lin. taken near St Malo × 1. From Boulenger.

1. Dorsal fin. 2. Tail showing myotomes. 3. Hind-limb.

secretion." The substances poured into the blood by both these organs are essential to the proper conduct of metabolism, that of the adrenal bodies being stimulating to the muscular tissues in particular.

The eggs develop entirely outside the body, and there is a large thin-walled swelling of the oviduct in which the ripe eggs accumulate just before being discharged. The male clasps the female round the waist and remains in this position sometimes for weeks, uttering loud croaks at intervals until the eggs are discharged. When the eggs are discharged he emits the spermatozoa on to them. The croaks are made by pumping the air from the lungs through the glottis into the pharynx and *vice versâ*. The pharynx has in *Rana esculenta* two side pouches, the vocal sacs, which become inflated with air. It is thus possible for this frog to croak when under water.

The development is in many respects different from that of Urodela. Soon after the young are hatched they acquire, it is true,

three external gills on each side, but there is no trace of limbs and the gill-slits are closed, each being represented by two closely adherent layers of epithelium, and as the mouth does not open into the alimentary canal no food is taken. Later the gill-slits become open; but a flap of skin, the gill-cover, grows back from the second visceral arch (the hyoid) and covers up the gill-slits and the external gills. The external gills then soon disappear. The two gill-covers unite with one another beneath the animal, so only one little opening to the gill-chamber remains, usually on the left side. The mouth has by this time opened into the alimentary canal, and it is provided with two horny ridges, one above and one below, besides rows of little horny prickles. The horny jaws crop the water-weeds upon which the tadpole lives.

The larva is now the well-known tadpole, with a rounded body and a long flat tail, with which it swims. The limbs gradually grow, but for a long time the front limbs are hidden beneath the gill-cover. When they finally burst through the animal sheds its horny jaws and leaves the water. For a short time the tail is retained, but absorption soon removes all trace of it and the development is complete.

Classification.

The Anura are divided into two main groups according to the development of the tongue. In the Aglossa it is entirely absent and the two Eustachian tubes have a common opening into the pharynx. This curious group only includes two genera. In one species, *Pipa americana*, the Surinam Toad, the eggs are emitted from the protruded oviduct on to the back of the female, and here the young pass through the tadpole stage enclosed in deep pockets of the moist skin. This species as its popular name implies is an inhabitant of S. America. In the Phaneroglossa, on the other hand, the tongue is well developed, being usually free behind, and in this case used to flick the prey, which consists of insects, into the capacious mouth. The Eustachian tubes are separate. The Phaneroglossa are divided into the Arcifera and the Firmisternia. In the first division the two epicoracoids of each side overlap (Fig. 272, B) and the two halves of the pectoral girdle are slightly movable on one another; in the second they are firmly united in the middle line (Fig. 272, A). The first division includes several families, but the two largest and most important are those of the Toads or Bufonidae and the Tree Frogs or Hylidae.

The Toads have no teeth whatever: their wrinkled skin is beset with wart-like poison glands in the upper parts, while numerous

little horny spines occur superficially in the epidermis. They only enter the water at the breeding season and Toads are in many respects more adapted to a land life than are Frogs. Two species live in Great Britain; *Bufo vulgaris*, found everywhere, and *Bufo calamita*, the Natterjack, a species with comparatively feeble hind-limbs, which crawls and does not jump. The Natterjack frequents sandy places and is thus local in its distribution.

The Bufonidae and several other families of Anura are stated by septematists to have "dilated diapophyses." By this term is meant broadened sacral ribs; this broadening indicates a possibility of back and forward play of the rib on the ilium, and points to a use of the hind limbs in crawling as opposed to the purely leaping movements of the frog. One species of Bufo (*B. americana*) is found in the north of North America. But besides the Bufonidae another family of the Arcifera, the Pelobatidae, which have teeth, is represented in North America by *Scaphiopus*, a burrowing species and on the continent of Europe by a closely allied genus *Pelobates*: both genera are provided with a sharp spur on the inner side of each foot, whence the name "Spadefoot" Toad which is bestowed on both.

In another family the Discoglossidae the tongue is a round cushion which is non-eversible. To this family belongs *Alytes* the celebrated midwife toad. The male and female pair on land, the male receives the egg-strings as they issue from the female, winds them round his legs and keeps them there till the young hatch, which they do in a much more advanced stage of development than do the tadpoles of other toads.

The Hylidae have teeth on the vomers and on the upper jaw, but their most remarkable peculiarity consists in the possession of fleshy cushions underneath the terminal joints of the digits, the bones of which are bent up and claw-like. By means of these cushions the Hylidae are able to adhere to smooth vertical surfaces, and so climb trees, in which they mostly live, only approaching the water for the purpose of laying their eggs. There is no species of this family in Great Britain and only one in Europe. In North America there are several species belonging to three genera; *Hyla*, *Chorophilus*, and *Acris*.

The Firmisternia have the two epicoracoids fused in the middle line and include the Frogs or Ranidae. There is only one species, *Rana temporaria*, which is here taken as the type of the Anura, really native to Great Britain, but there exist a few colonies of the common European species, *Rana esculenta*, mostly in the Eastern Counties. The Frogs of this species are most powerful croakers, and as their name implies they are used as food. It is

believed that they were introduced by monks from Europe, who before the Reformation used to pay periodical visits to England to supervise their property.

In Canada and the Northern United States there are eight species of Frogs. A species believed to be identical with *Rana temporaria* is found, but the two commonest are *Rana virescens*, of a green ground colour with lines of velvety black patches, and the great Bull-frog, *Rana catesbiana*, which attains three or four times the size of *Rana temporaria*, and is of brownish-yellow colour, peppered over with minute black dots. Like *Rana esculenta* this is essentially a water-frog whereas *Rana virescens* like *Rana temporaria* spends much of its time on land. *Rana catesbiana* is highly valued as a delicacy for the table, and in Canada it is being hunted so much that it is becoming rarer. *Rana esculenta* as its name implies is extensively eaten on the Continent of Europe and in France it is bred for the table on special farms.

Order III. **Apoda.**

The order Apoda is, as has already been mentioned, distinguished by the entire absence of limbs and the worm-like appearance and habits of its members. In the skeleton the retention of a complete roof of bones over the space between cranium and upper lip, known as the temporal fossa, and the existence of minute bony scales embedded in the dermis, are features retained from the Stegocephala. In accordance with their retiring burrowing habits the members of this order have very small eyes, which in some cases are rendered quite functionless by being concealed under the skin. The internal anatomy is in many respects like that of the Urodela, but the pulmonary arterial arch does not in all cases join the aorta. These animals often live at some distance from water and the larval development is passed through inside the egg-shell, but even there the embryo develops large external gills. The species of this family are restricted to the tropics; *Ichthyophis* is found in India, *Coecilia* in South America, and *Hypogeophis* in Africa. The extinct Stegocephala have been alluded to many times. Under this comprehensive head are comprised all the fossil Amphibia, remains of which are found in the Coal Measures and the Red Sandstones overlying them. It has been already pointed out that some of them, like *Branchiosaurus*, appear in the structure of the vertebral column to be the forerunners of the Urodela, while others, like the *Labyrinthodonta*, appear to lead on to the Anura. Besides

these, limbless forms are also known, and there seems to be some probability that these were the ancestors of the Gymnophiona. Hence within this ancient group the beginnings of the division of the Amphibia into the three orders by which it is now represented had already shown themselves.

The class of recent Amphibia is divided as follows:

Order I. **Urodela.**

Amphibia retaining throughout life a long tail.

Sub-order 1. **Ichthyoidea.** Urodela retaining throughout life external gills or gill-slits or both.

Family (1) Amphiumidae.

Both the upper and lower jaws are furnished with teeth. Fore- and hind-limbs small. Eyes small and devoid of lids. The gill-slits are in a vanishing state, and the gills disappear in the adult.

Ex. *Amphiuma*, *Cryptobranchus japonicus*, *C.* (*Menopoma*) *alleghaniensis* (the Hell-bender).

Family (2) Proteidae.

Both the upper and lower jaws with teeth. Eyes without lids. Maxillary bones absent. With permanent gills.

Ex. *Proteus*, *Necturus* (the Mud-puppy or "Water-lizard").

Family (3) Sirenidae.

Both jaws are toothless. The hind-limbs, the maxillary bones and the eyelids are absent. With permanent external gills.

Ex. *Siren*.

Sub-order 2. **Salamandroidea.** Urodela which in the adult stage lose all trace of gills and gill-slits.

Family Salamandridae.

Both the upper and lower jaws are furnished with teeth. Fore- and hind-limbs well developed. Eyes with movable lids.

Ex. *Molge*, *Salamandra*, *Desmognathus*, *Plethodon*, *Amblystoma*.

Order II. **Anura.**

Amphibia which lose when adult all trace of tail, hind-limb much more powerful than the fore-limb and used for leaping.

Sub-order 1. **Aglossa.** Anura devoid of a tongue. Eustachian pouch single and median.

Ex. *Pipa.*

Sub-order 2. **Phaneroglossa.** Anura with well-developed tongue. Eustachian pouch double.

Group I. **Arcifera.**

Phaneroglossa in which the epicoracoids of opposite sides overlap.

Family (1) Discoglossidae.

Arcifera with a round disc-shaped tongue, adherent at the whole of its base; vertebrae opisthocoelous. Teeth in the upper jaw only.

Ex. *Alytes, Discoglossus, Bombinator.*

Family (2) Pelobatidae.

Arcifera with a protrusible tongue, dilated sacral ribs and with teeth in the upper jaw only.

Ex. *Pelobates, Scaphiopus.*

Family (3) Bufonidae.

Like the previous family, but without any teeth.

Ex. *Bufo.*

Family (4) Hylidae.

Arcifera with dilated sacral ribs, with teeth in the upper jaw and adhesive discs on the fingers and toes.

Ex. *Hyla, Chorophilus, Acris.*

Group II. **Firmisternia.**

Phaneroglossa in which the epicoracoids are firmly united in the middle line.

Family (5) Ranidae.

Firmisternia with cylindrical sacral ribs.

Ex. *Rana.*

Order III. **Apoda.**

Amphibia of worm-like appearance, without limb or tail and with vestigial eyes.

Ex. *Coecilia, Hypogeophis, Ichthyophis.*

GLOUCESTER

CHAPTER XXII

SUB-PHYLUM IV. CRANIATA

Division II. Gnathostomata

Introduction to Amniota

The three classes of Craniata, termed Amniota, agree, as their name implies, in the possession of an amnion. This is a portion of the egg which is transformed into a hood by which the body of the embryo is enveloped, and which is thrown off at birth. But there are many other features which Amniota possess in common, and which suffice to show that they are all sprung from a single stem of primitive land animals, distinct from that which gave rise to Amphibia. All possess an allantois. This is a structure developed as a ventral outgrowth from the hind gut and homologous with the bladder of Amphibia, but in the Amniote embryo it is enlarged and extends between the limbs of the fold which constitutes the amnion, and it functions as an embryonic respiratory or nutritive organ, and this portion of the allantois is cast off at birth, only the stump remaining to serve as the bladder in the adult. No such modification of the bladder occurs in any Amphibian. The vertebral column of Amniota is also formed in a totally different way from that in which the vertebral column of Amphibia is constructed. The basiventral arch-piece of which the rib is an outgrowth does not enter into the formation of the centrum at all, but forms instead an intervertebral cartilaginous pad, which very rarely becomes ossified, and then forms a distinct bone called the subvertebral wedge-bone. The centrum is formed from the ventral intercalary piece, precisely that piece which is totally absent in the vertebral column of the Frog, and only present as an element in the intervertebral cartilaginous disc of Urodela. To the ventral intercalary the two basidorsals forming the neural arch become

attached. Therefore it is roughly true to say that the centrum of Amniota corresponds to the intervertebral cartilage of Urodela and *vice versâ.* The cartilaginous basiventral of Amniota is an insufficient support for the rib when this becomes heavy, and hence not only is a transverse process (diapophysis) developed from the neural arch which joins a "tubercular" process on the rib, and thus forms an additional support for it, but the proximal

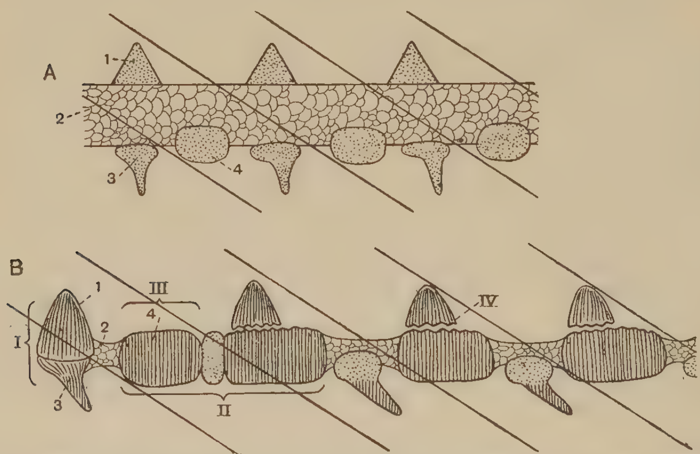

FIG. 278. Two stages in the development of the front part of the vertebral column of an Amniote (the Lizard).

A. Stage in which basidorsals, basiventrals and intercalaries are separate.

B. Stage of the completed vertebral column—the first four vertebrae are shown.

1. Basidorsal 2. Notochord. 3. Basiventral. 4. Ventral intercalary. I. Atlas vertebra formed by union of basidorsals and basiventrals. II. Axis vertebra formed from the second intercalary with the first intercalary attached to it as odontoid process. III. Third vertebra. IV. Fourth vertebra. Dotting, cross-hatching, etc. as in Figs. 232, 242, 254 and 267.

end or head of the rib is broadened and becomes attached to the centre (ventral intercalaries) before and behind it, and sometimes even becomes shifted so as to be completely attached to one of them. Even in this case, however, the rib betrays its origin by being attached to one end of the centrum, not as in Fish and Urodela to the middle of the centrum.

All Amniota agree in possessing a neck. This is a region of the body supported by a varying number of vertebrae which intervenes between the head and the heart. No trace of a neck is found

in any Fish or Amphibian. The first vertebra of the neck which is termed the atlas is formed in a different way to the rest: it has the form of a ring and it is constituted by the union of the first pair of basiventrals with the first pair of basidorsals. The first ventral intercalary forms a cylindrical centrum to which no neural arch is attached, but which becomes attached to the next centrum as the so-called odontoid process; this projects forwards through the ring formed by the atlas. The vertebra bearing the odontoid process is termed the axis vertebra, and all the rest of the vertebrae of the neck are termed cervical vertebrae (Fig. 278). There is great reason to believe that these vertebrae, like the neck region generally, have been formed by a process of intercalary growth: because of their peculiar relations to the chain of sympathetic ganglia. In primitive Vertebrates there is one sympathetic ganglion attached to each spinal nerve, but in animals with a neck there are only two cervical sympathetic ganglia: an anterior one (the so-called superior cervical ganglion) connected with the first cervical spinal nerve, and a posterior one (the so-called inferior cervical ganglion) connected with the last cervical nerve. The intervening region of the neck is totally devoid of sympathetic ganglia, and seems therefore to be a new formation.

The brain of Amniota has twelve, not ten pairs of cranial nerves, i.e. two additional pairs to the ten found in Pisces and Amphibia. The second of these two pairs corresponds to the hypoglossal nerve of the Frog, which in that animal emerges behind the first vertebra. It follows that the cranium of Amniota must have at least two more vertebrae amalgamated with it than are comprised in the cranium of Amphibia. In all Amniota the cranium is ossified in its hinder region by four bones, viz., the supra-occipital bone, an exoccipital at each side and a basi-occipital below. In no Amphibian are basi-occipital and supra-occipital elements developed. In the buccal cavity we have shelf-like outgrowths from the sides—the palatal flaps which divide the cavity more or less completely into an air passage above and a food passage below. In the pelvic girdle, in addition to ilium and ischium, there is a third bone below and in front termed the pubis. In the heart the conus has completely disappeared as a division of the heart. It is cleft to the base into "aortic arches," of which one conveys impure blood to the lungs. In the ventricle there is a flap-like outgrowth from the ventral wall which divides its cavity completely or incompletely into two compartments.

In the kidney the mesonephros or sexual part is completely separated from the metanephros, or non-sexual part, and the duct of the latter, the ureter, is formed in a different manner from that in which the metanephric duct or ducts of Urodela and Elasmobranchii are constituted. For whereas the metanephric ducts of these two groups are formed by a longitudinal splitting of the archinephric duct which separates the hinder kidney tubules from the sperm-carrying portion of the duct, the ureter of Amniota is formed as a flask-shaped evagination or outpouching of the archinephric duct primitively at right angles to its course. The body of the flask forms a cavity of the kidney termed the pelvis of the kidney, round which the metanephric tubules are grouped and into which they open; the neck of the flask which becomes continually lengthened forms the ureter; and the lower short part of the archinephric duct, common to it and to the sperm duct, becomes absorbed into the cloaca so that both ducts open independently of each other (Fig. 216). When we review this list of differences we see that whereas some of them could be regarded as evolutions of and improvements on the Amphibian type of structure, yet there are others, such as the constitution of the skull and the vertebral column, in which evolution seems to have gone on independently in Amphibia and Amniota, and to find a common starting-point for the two lines, we must go back to the very oldest land animals. Amongst the extinct creatures termed Stegocephala and reckoned as Amphibia, the earliest had no centra and the arch-pieces remained separate, and in some of these there is some evidence that the basi-occipital element in the skull was ossified and that the ventral intercalary was becoming large and important, and amongst these we must look for the ancestors of Amniota and the point of cleavage of the stock of land animals into two divergent stems.

CHAPTER XXIII

SUB-PHYLUM IV. CRANIATA

DIVISION II. GNATHOSTOMATA

SUB-DIVISION II. AMNIOTA

CLASS III. REPTILIA

THE name Reptile denotes literally anything that crawls (Lat. *repo* or *repto,* I crawl). Zoologically the term denotes the lowest Amniota, which are cold-blooded, and whose eggs are large and provided with plenty of yolk.

Perhaps the most characteristic feature of Reptiles is the nature of their skin. They are typically covered with scales which are widely different from the scales of fish. The latter are essentially areas of the dermis hardened by the deposition of lime with sometimes the addition of a layer of crystals from the basal ends of the ectoderm cells (enamel).

The scale of the Reptile on the contrary is nothing but an area of the horny layer of the skin where the cells are converted into horn or keratin and are adherent to one another. In the mass of the scale the horn is rendered brown by the presence of pigment, but the outermost layer is composed of clear cells and is known as the e p i t r i c h i a l layer. A corresponding layer covers the embryos of Birds and Mammals, but is shed before birth. A s l o u g h i n g or ecdysis of the scaly epidermis is a constant feature of the Reptilia. It may take place bit by bit, or as is the case with many Sauria the whole "skin" is cast in one piece (Fig. 279).

In very many living Reptiles, and in a great many extinct ones, there are numerous small dermal bones embedded in the skin termed o s t e o d e r m s. These do not belong to the same series of membrane bones as those which give rise to the dermal bones of the skull or the scales of fish. They are to be looked upon as later and secondary ossifications of the dermis arising long after the primary series had become separated from the skin and sunk inwards. In many

Reptiles osteoderms extend over and cover the dermal bones of the skull.

Another characteristic of Reptiles is that the skull articulates with the vertebral column by one condyle only.

The dermal glands so characteristic of the Amphibia have almost totally disappeared, being restricted to a small area, as, for instance, the front of the thigh in a Lizard. It follows that a Reptile is essentially a dry-skinned animal and by no means a "slimy beast."

The lungs have to some extent acquired a spongy texture, and the mechanism for inhaling and exhaling air is usually to be found in the ribs, not solely in the hyoid or remains of the hinder

Fig. 279. Section through the scale of a Lizard.

1. Epitrichial layer. 2. Heavily cornified cells forming the scale. 3. Pigment cell. 4. Ordinary cells of horny layer. 5. Innermost Malpighian layer. 6. Dermis.

visceral arches as in the Amphibia, although these may co-operate in assisting respiration.

Living Reptiles are divided into four orders, of which one consists of only one species, *Sphenodon punctatus*, found in New Zealand. This animal is the type of the order (i) **Rhynchocephala**, and is especially interesting as not only being to some extent intermediate in structure between other orders of living Reptiles, but as recalling very closely the structure of some of the oldest fossil Reptiles known to us. The other orders are (ii) the **Sauria** including (*a*) **Lacertilia** (Lizards), and (*b*) **Ophidia** (Snakes), the (iii) **Chelonia** (Turtles and Tortoises) and the (iv) **Crocodilia** (Alligators and Crocodiles). Of the four orders only the second and third are represented in Great Britain and these

by very few species; in North America the last three are well represented.

Structure of Lacerta.

As type we may select the common lizard, *Lacerta vivipara*, which may be seen on very warm days disporting itself in sandy and stony places in the south of England. On the Continent it and allied species are far more abundant: in the south of Europe in summer the whole country is alive with lizards. Almost every step in the country causes two or three specimens to rush rapidly away into some retreat, either a hole under a stone or a cleft in the bark of a tree.

The English lizard has roughly the shape of a Newt, but there is a distinct neck region in front of the fore-limb, and the limbs are sufficiently powerful to completely raise the belly well above the ground and also to run at a comparatively rapid rate. Both manus and pes have five digits which end in sharp claws. The body is covered all over with minute scales (Fig. 279), of which the prevailing colour is reddish-brown above, and orange passing into yellow beneath. On the ventral surface and the top of the head the scales are larger and arranged in pairs. The ear-drum is situated at the bottom of a slight pit, which is the first appearance of the outer ear. It is not developed in all Reptiles.

The anal opening is a transverse slit at the root of the tail behind the hind pair of legs. In front of the thigh the scales are perforated by a row of pores, the openings of the only dermal glands which the lizard possesses.

Skeleton.

Turning at once to the skeleton, we find that the vertebral column consists of procoelous vertebrae. All the vertebrae articulate with one another by overlapping facets called pre- and postzygapophyses as in Amphibia. Although externally similar to the vertebrae of Amphibia, the vertebrae of the lizard and of Reptiles generally are formed of different elements, as has been explained in the section dealing with Amniota. It is a characteristic of the lizard that the basiventral arch-pieces, which form the cartilaginous intervertebral pads in all Amniota, are partly ossified, and therefore appear in the dried skeleton. In the region of the neck they are termed subvertebral wedge bones or intercentra. In the region of the tail they form definite haemal arches and are known as chevrons. The rib has shifted its position so that the capitulum is attached

to the front end of the centrum (ventral intercalary) behind the basiventral to which it belongs. The tubercular attachment is represented by ligament. There are two sacral vertebrae which have expanded transverse processes with which the ribs are fused. Behind these come the vertebrae of the tail—the caudal vertebrae. Each of these bones is made up of two halves, an anterior and a posterior, which are but loosely connected with one another. The consequence is that when a lizard is seized by the tail this organ in many species snaps in two, one of the vertebrae breaking into an anterior and a posterior half.

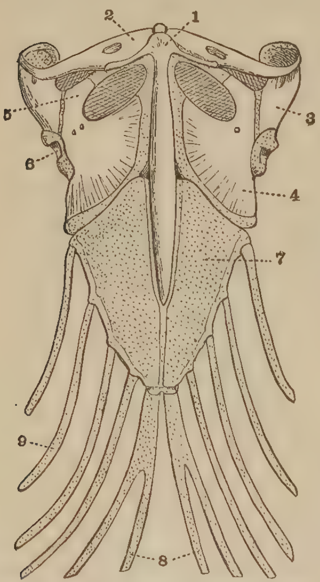

Fig. 280. Ventral view of the shoulder-girdle and sternum of a Lizard, *Loemanctus longipes* ×2. After Parker.

1. Interclavicle. 2. Clavicle. 3. Scapula. 4. Coracoid. 5. Precoracoidal process. 6. Glenoid cavity. 7. Sternum. 8. Sternal bands not united. 9. Sternal rib.

All vertebrae in front of the sacrum, except the first two, have distinct ribs attached to their transverse processes. In young specimens it can be seen that the odontoid process is separated from the second centrum, with which it ultimately fuses, by a cartilaginous pad representing the second pair of basiventrals, the first pair of basiventrals forming, as has already been explained, the ventral portion of the atlas vertebra, to be separated from the centrum of the second vertebra by an unossified disc representing the second pair of basiventrals (Fig. 278).

The ribs in front of the pectoral girdle remain quite short; this region is the cervical or neck region. Immediately behind the pectoral girdle the ribs are very long and curved so as to half encircle the body like the hoops of a barrel. The foremost have attached to their lower ends cartilaginous bars termed the sternal ribs, which are in turn united with a cartilaginous sternum in the middle line. This structure has the form of a lozenge-shaped plate with a hole in the middle, ending behind in two forks to which some of the posterior sternal ribs are attached. The front portion of the

sternum corresponds to the sternum of Amphibia, but the forks behind, which are termed sternal bands, are formed by the union of the ventral ends of the sternal ribs of one side with one another.

The skull is distinguished from the Amphibian skull by many features. The jaws do not arch outwards at the sides of the cranium, as in the Frog, but are bent inwards underneath it. Behind, the cartilage of the cranium is completely replaced by four bones—by the supra-occipital above the foramen magnum, the exoccipitals at the sides of this opening, and the basi-occipital beneath. This last bone bears a single knob or condyle which articulates with the atlas vertebra. To the formation of this condyle the exoccipitals in some degree contribute. The basi-occipital and the single condyle are highly characteristic of all Reptilia. In common with all Amniota Reptilia possess a supra-occipital and a basisphenoid bone. The last-named is a bone replacing the cartilaginous floor of the cranium just in front of the basi-occipital. The parasphenoid so characteristic of Amphibia is reduced to a mere splint attached to the front of the basisphenoid.

The anterior part of the cranium is so compressed between the large eyes that its cavity completely disappears and it becomes replaced by a vertical sheet of membrane, the interorbital septum. It follows that in the dried skull the two orbits apparently open widely into one another. Almost the entire brain is pushed back behind the eyes into the hinder part of the cranium. Only the olfactory stalks run through holes in the upper part of the septum. The orbitosphenoid of Urodela and the sphenethmoid of the Frog are quite unrepresented, though in some of the larger Lizards allied to Lacerta there is a minute orbitosphenoid bone in the upper part of the interorbital septum (31, Fig. 281). The interorbital septum is certainly a characteristic of the primitive Reptilia. It has however been lost in some of the most recent and highly modified forms.

The auditory capsule as in Teleostei is completely converted into bone, but it is ossified by three bones only, an epi-otic above, which fuses with the supra-occipital, an opisthotic behind, which joins the exoccipital, and a pro-otic which remains distinct. There is no trace of the pterotic bone so characteristic of Teleostei.

As in Amphibia the first visceral arch is represented by an upper half consisting of a suspensorium with a pterygoid process, and a lower half—Meckel's cartilage. In the upper half, however, the cartilage is completely replaced by bone. The suspensorial portion forms the quadrate bone, which is attached to the side of the

auditory capsule. The pterygoid process is completely ossified by the pterygoid bone behind and the palatine in front.

A curious bone, characteristic of many of the Lacertilia, is the epipterygoid or columella cranii, which runs from the pterygoid

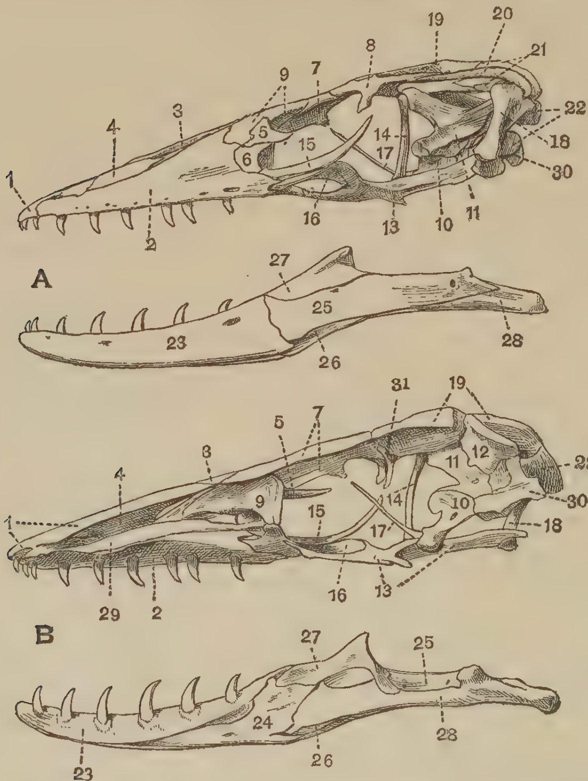

FIG. 281. A. lateral view, and B. longitudinal section of the skull of a Lizard, *Varanus varius* × $\frac{3}{5}$.

1. Premaxilla. 2. Maxilla. 3. Nasal. 4. Lateral ethmoid. 5. Supra-orbital. 6. Lachrymal. 7. Frontal. 8. Postfrontal. 9. Prefrontal. 10. Basisphenoid. 11. Pro-otic. 12. Epi-otic. 13. Pterygoid. 14. Epipterygoid (columella cranii). 15. Jugal. 16. Transverse bone. 17. Parasphenoid. 18. Quadrate. 19. Parietal. 20. Squamosal. 21. Supratemporal. 22. Exoccipital. 23. Dentary. 24. Splenial. 25. Supra-angular. 26. Angular. 27. Coronoid. 28. Articular. 29. Vomer. 30. Basi-occipital. 31. Orbitosphenoid.

vertically up to the parietal. This bone is however found only in some Lacertilia, not in Reptiles generally.

The two pterygoid bones, instead of arching outwards, as in

Amphibia, converge under the base of the cranium towards the middle line, and they articulate with outgrowths from the basisphenoid, called basipterygoid processes. The palatines are united in front with the floor of the nasal capsule: they bear on their

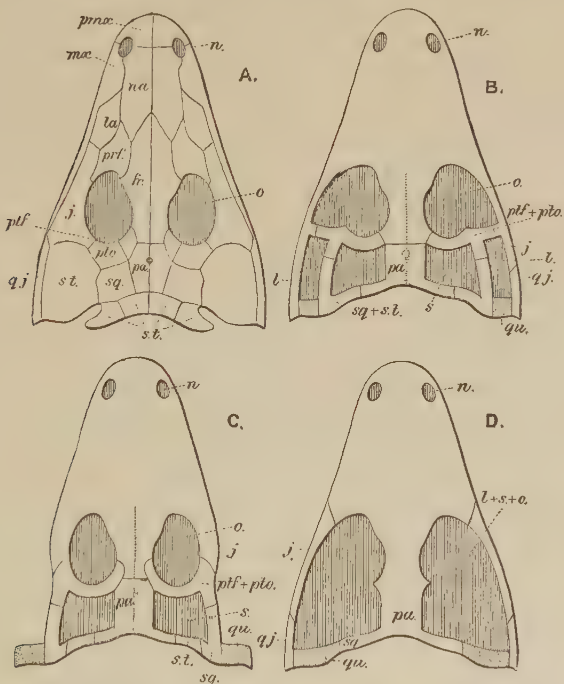

Fig. 282. Diagram of the cranial roof in a Stegocephalan, various types of Reptiles, and a Bird, showing modifications in the posterolateral region. From Smith Woodward.

A. Stegocephalan (*Mastodonsaurus giganteus*, about one-fifteenth nat. size, after E. Fraas). B. Generalised Rhynchocephalan and Crocodilian. C. Generalised Lacertilian, often losing even the arcade here indicated. D. Generalised Bird. *fr*. Frontal. *j*. Jugal. *l*. Lateral temporal fossa. *la*. Lachrymal. *mx*. Maxilla. *n*. Narial opening. *na*. Nasal. *o*. Orbit. *pa*. Parietal. *pmx*. Premaxilla. *prf*. Prefrontal. *ptf*. Postfrontal. *pto*. Postorbital. *q.j*. Quadratojugal. *qu*. Quadrate. *s*. Supratemporal fossa. *s.t*. Supratemporals. *sq*. Squamosal. Vacuities shaded with vertical lines, cartilage bones dotted.

inner sides slight ridges which project somewhat into the cavity of the mouth. These ridges support a pair of flaps of the lining of the mouth, the palatal flaps, which as we have seen are characteristic of all Amniota. In the lizard they remain unconnected

with one another and thence the division of the mouth cavity into an air-passage above and a food-passage below remains incomplete.

The end of Meckel's cartilage which articulates with the quadrate is converted into a bone, the articular. Three pairs of the hinder visceral arches are preserved. These retain their rod-like form as in Urodela, the median connecting pieces (copulae) remaining small.

The membrane bones of the skull are one of its most characteristic features. The roofing bones are the same as in the Urodela—paired nasals, frontals and parietals. On the roof of the mouth there are two vomers and a parasphenoid. The vomers, however, are rod-like, toothless and placed close together, and the parasphenoid is a small rudiment.

The bones of the side of the head and the upper lip form a most peculiar scaffolding which is widely separated from the cranium. The lizard is in an intermediate condition between the Cotylosauria or most primitive fossil Reptiles, in which as in the Amphibian Stegocephala a continuous sheet of bones extends from the cranium to the upper lip, and modern Amphibia, where all those bones have disappeared, leaving a large vacuity between the cranium and upper lip.

In front in the upper lip there is a premaxilla bearing teeth followed by a maxilla in which there are also teeth. The maxilla is joined to the pterygoid by an ectopterygoid or transverse bone. Between the maxilla and frontal on the side of the face are two bones known as prefrontal and lachrymal. The line of bones in the upper lip is continued by the jugal. This unites with a bone placed behind the eye termed the postfrontal, which joins both the frontal and parietal. Thus the eye is surrounded by a ring of bone. In some of the larger Lacertilia though not in *Lacerta* this ring is completed by a minute postorbital bone which intervenes between the jugal and postfrontal.

The squamosal is a characteristic V-shaped bone. The apex of the V articulates with the upper side of the quadrate: of the two arms one is directed forwards and meets the postfrontal, thus forming a bony bar parallel to the cranium which is called the upper temporal arcade. The other limb is directed backwards and inwards and meets a crest on the parietal so that a bridge is formed extending over the hinder part of the cranium. The limb seems to have been a distinct bone to which the name tabulare has been given. The space in the dried skull existing between this

bridge and the cranium is called the post-temporal fossa. In many Reptiles, including most Lacertilia, there is a similar space between the cranium and the lateral bridge formed by the junction of the squamosal and postfrontal which is termed the supratemporal fossa. This space is roofed over in Lacerta by two dermal bones called supratemporals which are not to be confounded with the bones bearing this name in Pisces. They are osteoderms, and the sole remnants of a once continuous covering of these bones.

Finally, the space intervening between the quadrate and jugal on the side of the face is known as the laterotemporal fossa. In *Sphenodon*, *Crocodilia* and a very large number of extinct Reptiles it is bounded below by a quadratojugal bone which joins the jugal to the quadrate. When the quadratojugal is present the series of bones consisting of maxilla, jugal and quadratojugal is known as the lower temporal arcade. The upper temporal arcade is formed as we have seen by the postfrontal and the squamosal. The loss of the quadratojugal in Lacertilia is doubtless connected with the greater mobility of the jaws. In some Lizards, notably in Geckos, the quadrate can move slightly on its articulation with the skull, as can also the pterygoid on the basipterygoid process. When the lower jaw is pulled downwards and backwards by its depressor muscle it tends to throw the lower end of the quadrate slightly forwards: the pterygoid slides on the basisphenoid, and pushing the ectopterygoid tilts the maxilla slightly upwards. With the maxilla all the other bones of the face move, and the membranous interorbital septum permits the ethmoidal region of the cranium to be slightly bent on the hinder portion.

The cartilaginous lower jaw is ensheathed by five distinct membrane bones. The dentary and splenial occupy the same positions as in Teleostomi and Urodela. The angular clamps the under side of the articular, which is the cartilage bone replacing the upper end of the cartilaginous jaw. The supra-angular lies above the angular on the outer side of the articular. The coronoid is a small projection on the upper edge of the jaw.

The pectoral girdle is at first sight exceedingly complicated, but in reality it consists of the same parts as in the Anura. Above the cavity for articulation of the arm—the glenoid cavity—there is the cartilaginous scapula; below the girdle forks into a coracoid and precoracoid united by an epicoracoid. The cartilage bones present are the scapula, precoracoid and coracoid. The cartilage above the scapular bone is slightly calcified but is not converted into

bone; this region as in Amphibia is called the suprascapula. Along the inner edge of the suprascapula, scapula and precoracoid runs a strong membrane bone, the clavicle, which reaches a median bone, the T-shaped interclavicle. This bone underlies the sternum. The two epicoracoid cartilages join the anterior edges of the sternum (Figs. 280 and 283).

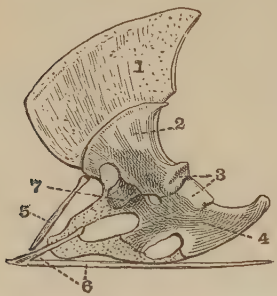

Fig. 283. Lateral view of the shoulder-girdle of *Varanus* ×⅚.

1. Suprascapula. 2. Scapula. 3. Glenoid cavity. 4. Coracoid. 5. Clavicle. 6. Interclavicle. 7. Precoracoidal process.

The space between the coracoid and precoracoid is called the coracoid fontanelle. Since in the Urodela it is not closed by an epicoracoid it may be regarded as a bay or indentation in the lower half of the originally simple pectoral girdle. The condition of affairs in Urodela throws considerable light on what occurs in certain other Lacertilia, such as the American Iguana. There we find that a similar deep indentation has become developed on the inner side of both scapula and coracoid, so that projections are formed to which the names mesoscapula and mesocoracoid have been given. These are not ossified by separate bones but are regions of the scapula and coracoid bones.

The fore-limb of the lizard might be taken as the type of the pentadactyle limb, since there are five fingers and the carpus has all the nine bones developed.

The pelvic girdle differs markedly from that of any Amphibian, in that in its lower portion there is a hole called the obturator foramen, corresponding to the coracoid foramen in the pectoral girdle. The girdle is ossified by three bones, viz., a vertical ilium articulating with the ribs of the sacral vertebrae, a pubis ossifying the anterior limb of the lower half of the girdle and an ischium ossifying the posterior limb. Both pubis and ischium meet their fellows in the middle line; such a union is termed a symphysis. The two obturator foramina are closed below and at the same time separated from one another by a longitudinal ligament which may have a certain amount of ossification in it. All three bones contribute to the formation of the acetabulum, the cavity for the articulation of the femur.

We have already pointed out that all Amniota possess a distinct

pubis ; all living Amniota also possess an obturator foramen but it is not present in some of the oldest fossil Reptilia.

On the hinder edge of the pubis there is a projection which is called the lateral process. In some extinct Reptiles this process was extraordinarily long and ossified by a distinct bone, which has been called the postpubis. It is the postpubis which forms the so-called pubis of Birds and Mammals.

The most marked feature of the hind-limb is the formation of a sharply-marked "ankle" joint. There is one place and one only where the foot bends on the shank ; whereas in Urodela bending can occur at any place in the mosaic of small bones which forms the tarsus.

In the lizard all the three upper bones of the tarsus are joined to form a horizontal bar. The lower bones have almost entirely coalesced with the corresponding metatarsals, only the third and fourth of the series being distinguishable. Thus the lizard has what has been called an intertarsal joint—an arrangement which is highly characteristic of many Reptiles and of all Birds.

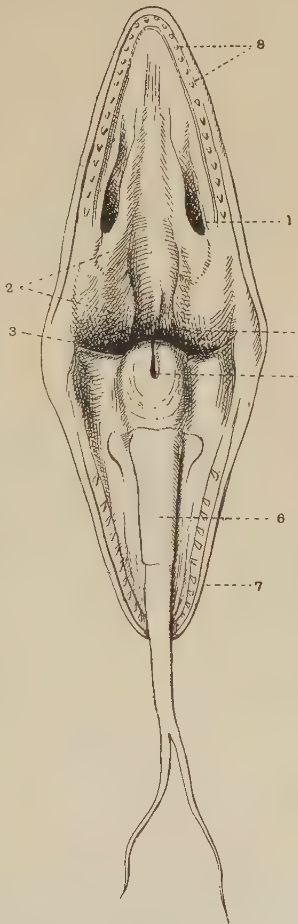

FIG. 284. Open mouth of *Varanus indicus* × 1.

1. Posterior or internal nares. 2. Palatal folds. 3. Internal opening of Eustachian tubes. 4. Opening of oesophagus. 5. Glottis. 6. Tongue half protruded. 7. Lip of lower jaw. 8. Teeth of upper jaw.

Viscera. All trace of the division of the abdominal muscles into myotomes has disappeared, but in the region of the ribs the innermost layer of the muscles of the flanks still retains the metameric arrangement and consists of a series of bands connecting each rib with its successor. These bands are termed the intercostal muscles and each consists of an external and an internal

layer of fibres. The fibres of the external layer slope upwards and forwards and, in contracting, cause the ribs to rotate forwards; the fibres of the inner layer slope upwards and backwards and have the reverse effect. Respiration is effected by the pulling forwards and backwards of the ribs by these intercostal muscles. In their relaxed condition the ribs slant strongly backwards. When they are pulled forward by muscles attaching them to the anterior vertebrae and by the external intercostals, they rotate forwards so as to stand out at right angles to the vertebral column and thus enlarge the cavity of the chest, that is, the coelom. The diminution of pressure in this air-tight cavity at once causes an inrush of air through the glottis, the elastic lungs are expanded and their walls closely follow the chest wall. It will be noticed that the mechanism of inspiration is very different from that of Amphibians (pp. 527, 555). The network of low ridges which is found already on the inner side of the Frog's lung has in the Reptile greatly increased in complexity. The primary ridges are much higher, and between them are lower secondary and even tertiary ridges: the cavity of the lung is as it were partly filled up by a spongy mass. In all Saurians however

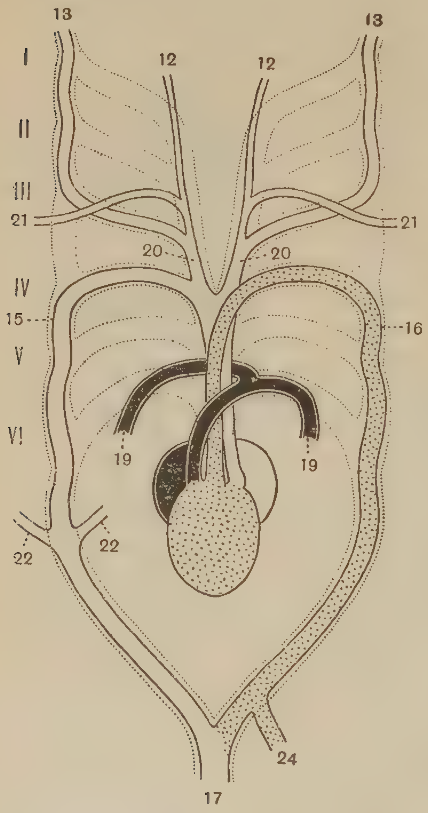

FIG. 285. Diagram of arterial arches of *Chamaeleo* viewed from the ventral aspect.

I, II, III, IV, V, VI. First to sixth arterial arches. 12. Tracheolingual (ventral carotid). 13. Common carotid (dorsal carotid). 15. Right systemic arch. 16. Left systemic arch. 17. Dorsal aorta. 19. Pulmonary. 20. Innominate. 21. Scapular (equivalent of subclavian of ventral type). 22. Subclavian (dorsal type). 24. Coeliac.

the central cavity is easily recognised as a wide space: whilst in Crocodiles and Tortoises, still more so in Birds and Mammals, it is represented only by the bronchial tubes.

The lungs are connected with the glottis by a comparatively long stalk, the trachea or windpipe, which is stiffened by rings of cartilage. A similar structure is found amongst Amphibia in the Gymnophiona and in a few Urodela. Immediately below the glottis the trachea is enlarged. The enlarged portion is stiffened by a large, broad, ring-shaped cartilage, the cricoid, to which are articulated two arytenoid cartilages. The whole structure consisting of the dilatation of the trachea and its cartilages is called the larynx.

The lizard like the Frog lives principally on insects and is provided with a long mobile tongue cleft at the tip, by means of which the prey are whisked into the mouth. The tongue is free in front and attached behind, so that in the lizard there is the opposite arrangement to what is found in the Frog. The teeth are simple and conical, and are implanted in a groove on the inner side of the bones bearing them. As the lizard grows they become actually fused with the bone along the side of the groove and as they are worn out they are replaced by others developed from the groove.

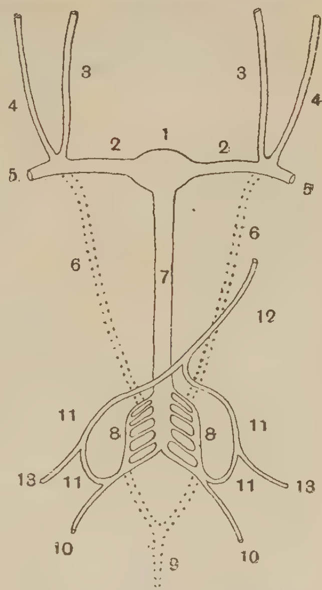

FIG. 286. Diagram to show arrangement of the principal veins in the *Anura* and *Reptilia*.

1. Sinus venosus, gradually disappearing in the higher forms. 2. Ductus Cuvieri = superior vena cava. 3. Internal jugular = anterior cardinal sinus. 4. External jugular = sub-branchial. 5. Subclavian. 6. Posterior cardinal, front part = vena azygos. 7. Inferior vena cava. 8. Renal portal = hinder part of posterior cardinal. 9. Caudal. 10. Sciatic = internal iliac. 11. Pelvic. 12. Anterior abdominal. 13. Femoral = external iliac.

When a Frog's mouth is forced open, amongst the most striking features of the roof of the mouth are the two large eyeballs shining through. When we open the mouth of a lizard nothing of the eyes can be seen. There is projecting inwards from the upper lip on each side a flap, the palatal

fold (2, Fig. 284). This does not meet its fellow in the middle line, a cleft existing between them. These folds conceal the eyeballs and the inner openings of the Eustachian tubes which lead up to the ear-drum. Palatal folds as already mentioned are found in all Reptilia.

Turning now to the circulatory system we find that the conus arteriosus no longer exists as such, having been cleft into three trunks down to its commencement in the ventricle. One of these trunks is ventral and slightly posterior to the others, and gives rise to the two arterial arches, which as pulmonary arteries supply the lungs and have no connection with the aorta. The other two arterial trunks form the right and left roots of the aorta. They cross each other at their origin, that which passes to the right of the oesophagus arising from the left of the ventricle and *vice versâ*. The third pair of arterial arches, corresponding to the carotid arches of Amphibia, are well developed in *Lacerta vivipara*. They have a common stem which arises from the right systemic arch. In some lizards the longitudinal epibranchial vessel of the embryo persists between the carotid and systemic arches on either side, so that in this respect a lizard may be even more primitive than a Newt, but this feature seems to be confined to the genus *Lacerta*. In other Lacertilia, and indeed in all other Reptiles, this connecting link has disappeared.

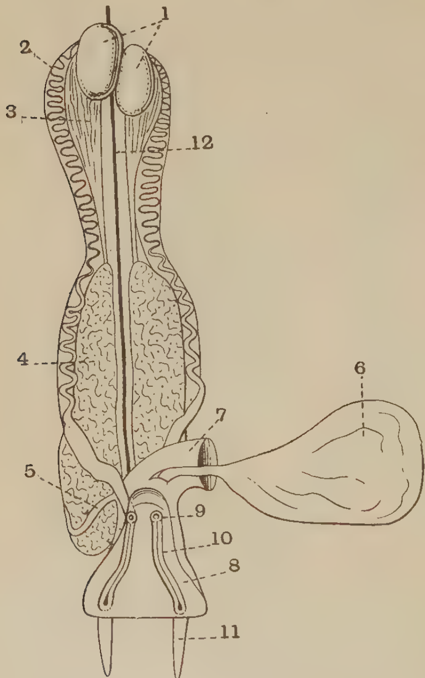

FIG. 287. Urino-genital organs of male Lizard.

1. Testis. 2. Vas deferens = archinephric duct. 3. Epididymis = (mesonephros). 4. Kidney = metanephros. 5. Ureter. 6. Bladder. 7. Rectum cut and turned back. 8. Cloaca laid open. 9. Opening of vas deferens. 10. Groove leading to opening of penis. 11. Penis. 12. Dorsal aorta.

The ventricle has projecting into its cavity two imperfect

partitions or septa. One is the continuation of the division between the two auricles, the other is a ridge which arises from the ventral side and tends to separate the opening of the pulmonary arteries from that of the right and left aortic arches. When the ventricle at first begins to contract it is full of venous blood from the right auricle: by the time arterial blood has commenced to enter it from the left auricle, the ventral septum mentioned above has been driven against the opposite wall, so as to shut off the pulmonary trunk from the rest of the ventricle and prevent its receiving any more blood. The left aortic arch, which arises on the right, receives mostly venous blood from the right auricle, whilst the right aortic arch arising on the left receives arterial blood from the left auricle, and it is from this arch, as mentioned above, that the carotid arteries arise. Hence the head receives comparatively arterial blood, and all the rest of the body mixed blood. The lingual artery of Amphibia is represented in Reptiles by a vessel (tracheolingual or "ventral carotid") which arises from the carotid arch near the middle line and supplies the tongue, trachea and muscles of the neck and shoulder.

The vessels supplying the fore-limb arise together from the right systemic arch in the case of Lizards instead of as in Anura from both right and left arches; they are subclavians of the dorsal type (see p. 431), but in Chelonians and Crocodiles the subclavians are ventral in origin, coming off from the carotid trunk on either side close to its division into ventral and dorsal carotids. In Lizards this "ventral subclavian" is represented by the scapular artery which runs to the shoulder region.

The veins, on the whole, closely resemble those of *Molge*. There is however no large cutaneous vein, and the external jugular veins are represented by a median inferior jugular vein which opens into the right anterior vena cava. The anterior part of the posterior cardinal, now called the vena azygos, is found only on the right side, where it receives the numerous intercostal veins, returning the blood from the muscles connecting the ribs. The renal portal, sciatic, femoral and anterior abdominal veins have the same arrangement as in the Urodela.

The brain is distinguished by the comparatively large size of the cerebral hemispheres, which overlap the thalamencephalon above and at the sides. They end in front in large pear-shaped olfactory lobes. The cerebellum is a high vertical ridge and is thus much more prominent than in any Amphibian. The remainder of the hind-brain,

the medulla oblongata, includes a longer portion of the spinal cord than it does in Amphibia, for the hypoglossal nerve arises from its side and escapes through an aperture in the exoccipital bone. This nerve is reckoned the twelfth cranial, not the eleventh, for there is a trunk called the spinal accessory or eleventh cranial, which arises by several roots from the side of the medulla oblongata, joins the vagus in a ganglion, and then leaving the skull supplies some of the neck muscles. In the Ophidia this nerve is not distinguishable from the vagus.

In the genital organs, the Lizards and Reptiles generally are distinguished from Amphibia by the complete separation of the mesonephros from the metanephros or functional part of the kidney. The persisting part of the mesonephros, now known as the epididymis, is only developed in the male, where it is closely connected with the testis. As in the Newt it receives the vasa efferentia. In the female the oviduct is shorter and has a wider internal funnel than in the Amphibia, and it is also placed further back so as to be rather nearer to the ovary. This is an arrangement suited to the large size of the eggs, which are too heavy to be drawn any distance by the current produced by the cilia of the oviduct.

The egg is fertilised whilst still in the oviduct. The male lizard has two organs called copulatory sacs or penes, situated, one on each side, on the hinder wall of the cloaca. These, when not in use, are hollow pouches opening into the cloaca. When in use they are turned inside out, and are then seen to have grooves leading to the openings of the vasa deferentia or archinephric ducts.

Most Lizards lay their eggs in crevices amongst stones and allow them to be hatched by the heat of the sun. In all cases a considerable amount of development goes on before they are laid. In the English species *Lacerta vivipara* the young burst through the egg-shell and use up all the yolk whilst they are still in the oviduct, so that in common parlance they are born alive, that is, as little lizards and not as eggs.

Order I. **Rhynchocephala.**

As mentioned above, the order Rhynchocephala is represented by the single species, *Sphenodon punctatus*, found only in New Zealand. This is a very Lizard-like animal. The back is covered with small scales which in the middle line form a comb-like crest: the belly is covered with large square scales. In the skeleton and

male genital organs, however, *Sphenodon* is widely different from the Lizard. The quadrate in the skull is quite immovable, being firmly clamped by the squamosal and quadratojugal. The laterotemporal fossa is thus completely bounded below and the supratemporal fossa is uncovered. The postorbital and tabulare bones are distinct. Between the parietals is a gap called the interparietal foramen: in this is situated the tip of the pineal body which has here all the characters of a simple eye.

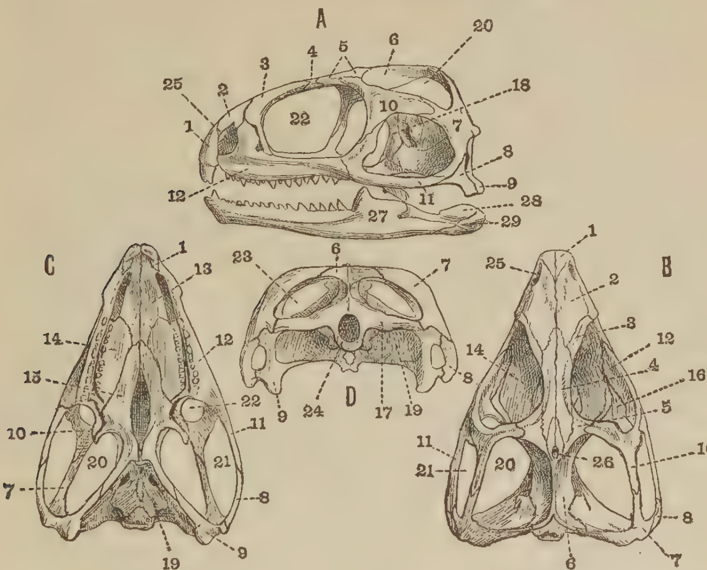

FIG. 288. Skull of *Sphenodon punctatus* × 1.

A. Lateral view. B. Dorsal view. C. Ventral view. D. Posterior view. After von Zittel.

1. Premaxilla. 2. Nasal. 3. Prefrontal. 4. Frontal. 5. Postfrontal. 6. Parietal. 7. Squamosal. 8. Quadratojugal. 9. Quadrate. 10. Postorbital. 11. Jugal. 12. Maxilla. 13. Vomer. 14. Palatine. 15. Pterygoid. 16. Ectopterygoid or transverse bone. 17. Exoccipital. 18. Epipterygoid. 19. Basisphenoid. 20. Supratemporal fossa. 21. Lateral temporal fossa. 22. Orbit. 23. Posttemporal fossa. 24. Foramen magnum. 25. Anterior nares. 26. Interparietal foramen. 27. Dentary. 28. Supra-angular. 29. Articular.

The animal has teeth when young, but they become worn away, while the edges of the maxilla and premaxilla become converted into cutting edges.

The vertebrae are amphicoelous, i.e. in the dried state, since distinct joints are not formed and the intervertebral cartilage

persists in an undivided condition between throughout life. The ventral portion of these cartilages, however, are ossified and appear as the subvertebral wedge bones and chevrons, beneath the interspaces between the vertebrae throughout the neck, trunk and tail, and not as in Lizards in the neck and tail regions only.

The ribs have three divisions, there being a small intermediate piece intercalated between the dorsal and sternal rib. From the dorsal rib a hook-like outgrowth, the uncinate process, projects backwards, which overlaps the next rib as in Crocodiles and Birds.

Behind the sternum there is a long series of rod-like bones, the so-called abdominal ribs, embedded in the muscles of the belly. They are placed parallel to the direction of the sternal ribs, that is, they slope obliquely forwards and inwards. They are regarded as membrane bones and supposed to correspond to the ventral bony scales of the Stegocephala; they are probably of older origin than the osteoderms which underly the scales in many Reptiles and are not directly homologous with them.

All these peculiarities of the skeleton are found in many of the oldest fossil reptiles.

There is no proper copulatory organ: the cloaca is used for this purpose as in the Urodela.

Numerous fossil Reptiles with skulls quite indistinguishable from that of *Sphenodon*, or differing from it only in unimportant particulars, are found in the Triassic Rocks. They are known as Diapsid (Gr. δίς, doubly; ἀψίς, an arch) Reptiles because, as already explained, the remnants of the once continuous covering of membrane bones persist as two temporal arches, or arcades, an upper postfronto-squamosal and a lower jugal-quadratojugal arcade. From such primitive Diapsid Reptiles modern Lizards, Snakes and Crocodiles, as well as *Sphenodon*, are descended. The modern descendants of this primitive stock have diverged in two directions.

On the one hand, the original stock gave rise to descendants with long flexible bodies and extensible jaws—this latter feature involving of course a movable quadrate. The cloacal opening became converted into a transverse slit and copulatory organs became developed behind it. This stock includes the Snakes and Lizards which are often included in the one comprehensive order the Sauria.

On the other hand, the descendants of the common ancestral form diverged in the direction of heavily armoured forms, in which membrane bones underlying the scales were developed and in which

the jaws are very powerful, the quadrate remaining immovably clamped by the quadratojugal. The cloacal opening became a longitudinal slit and developed the single median copulatory organ on its front wall. This stock includes the Crocodiles. The Chelonia or Turtles and Tortoises are probably descended from Monapsid Reptiles, of which numerous remains occur side by side with those of Diapsid Reptiles. In Monapsid Reptiles there is only one temporal arch constituted of jugal, quadratojugal, postfrontal and squamosal and one temporal fossa above it, which corresponds to the supero-temporal fossa of Diapsida. Chelonia resemble Crocodilia in the cloaca and copulatory organ.

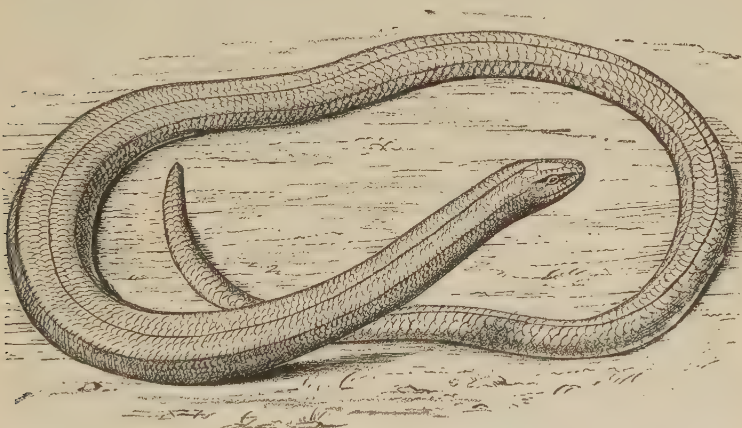

FIG. 289. A limbless Lizard, *Anguis fragilis*, the Blind-worm, slightly reduced.

Order II. **Sauria.**

We now turn to the Sauria. Most people would imagine that the task of distinguishing a Lizard from a Snake was an easy one. But if we were to collect together all the limbless species of Reptiles we should find not only that they differ very much from one another in the structure of the skull and in other points, but that they are more nearly related to different families of Lizards than to one another. There is no doubt that the snake-like forms have been derived from four-limbed reptiles like Lizards, for some of them have rudimentary vestiges of limbs. It is evident then that there must be an advantage in certain situations in getting rid of limbs, and it is further evident that the effect of this advantage has been that not only in one but in many families of Lizards

some species have lost their limbs. The kind of life to which a snake-like form is suited is a lurking one amongst crevices in stones, or thick vegetation, or in the soil, where movement is best effected by wriggling and limbs would be in the way.

Under these circumstances, we must either class together all limbless Sauria as Snakes, and thus give up the idea that the members of an order must necessarily be descended from the same ancestral species, or else we must select one group as the true Snakes (Ophidia), the members of which have some other characters in common besides the negative one of having no limbs. This latter course is that which has been adopted by Huxley, who defines true Snakes somewhat arbitrarily as those forms in which the two halves of the mandible are connected by elastic fibres, so that they can be widely divaricated from one another in the act of swallowing, and which have lost all trace of the pectoral girdle and of the urinary bladder, although they may retain traces of hind-limbs.

Sub-order 1. **Lacertilia.**

The Lacertilia then include all species of Sauria which have the right and left halves of the mandibles connected by a sutural symphysis and which retain a urinary bladder and some trace of the pectoral girdle. In all other characters they are a very diversified group. Most of them possess well developed limbs, movable eyelids and movable quadrate bones, but a good many species belonging to specialised burrowing families have no limbs and scarcely a trace of the pectoral girdle, while the eyes are concealed beneath the skin and the quadrate has become more or less immovable. Some, e.g., *Draco volans*, have the hinder ribs expanded so as to press out two expansions of skin and form a parachute-like expansion on each side, by means of which they are supported as they flit from tree to tree in great leaps. Most feed on insects, worms, etc. like the English Lizards; some are large enough to seize mice and birds and frogs. The limbless forms are represented in England by the Blind- or Slow-worm, *Anguis fragilis*, and in North America by the allied Glass-snake, *Ophisaurus ventralis*. These animals have skulls like that of *Lacerta* and rudiments of pectoral girdles. Besides the Blind-worm, the Common Lizard, *Lacerta vivipara*, and the Sand-lizard, *Lacerta agilis*, are British.

In North America four families of Lizards are represented, one being that of the limbless ANGUIDAE, while the most remarkable

of the others is that of the IGUANIDAE. These animals have short thick tongues and overlapping scales which form a crest of spines on the head and back and round the throat. *Phrynosoma douglasi*, the horned "toad," is found all through the Central States and even penetrates into Ontario; it is the sole Lizard found in Eastern Canada.

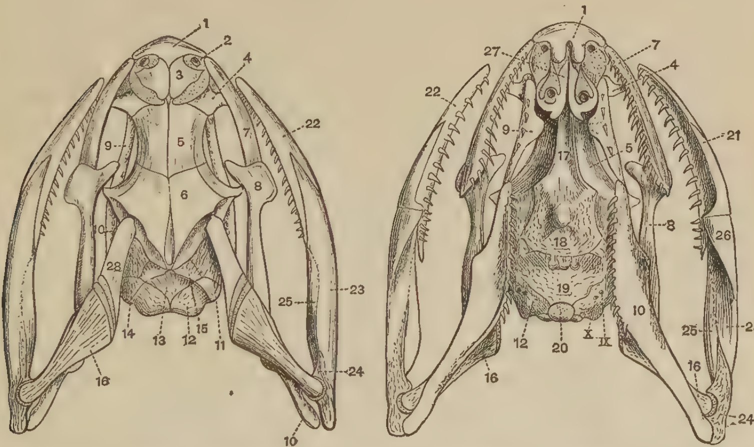

FIG. 290. Dorsal (to the left) and ventral (to the right) views of the skull of the Common Snake, *Tropidonotus natrix*. After Parker.

1. Premaxillae (fused). 2. Anterior nares. 3. Nasal. 4. Prefrontal. 5. Frontal. 6. Parietal. 7. Maxilla. 8. Transverse bone. 9. Palatine. 10. Pterygoid. 11. Pro-otic. 12. Exoccipital. 13. Supra-occipital. 14. Opisthotic. 15. Epi-otic. 16. Quadrate. 17. Parasphenoid. 18. Basisphenoid. 19. Basi-occipital. 20. Occipital condyle. 21. Splenial. 22. Dentary. 23. Angular. 24. Articular. 25. Supra-angular. 26. Coronoid. 27. Vomer. 28. Squamosal. IX, X. Foramina for the ninth and tenth cranial nerves.

Sub-order 2. **Ophidia.**

The Ophidia, or true Snakes according to definition, have the right and left halves of the mandible connected by an elastic band; they are also devoid of a urinary bladder and of any trace of a pectoral girdle. Besides this however they have a large number of other characters which severally are shared by some families of Lizards but which collectively are found only in the Ophidia.

The vertebrae in addition to the zygapophyses on the sides of the neural arch have median bosses and pits by which they fit into one another, called respectively zygantra and zygosphenes (Gr. *ἄντρον*, a cave or hollow; *σφήν*, a wedge). There

are no sternal ribs or sternum, but the dorsal ribs are elongated and curved ventrally, and a Snake literally walks on the ends of them; it is in a sense a vertebrate centipede.

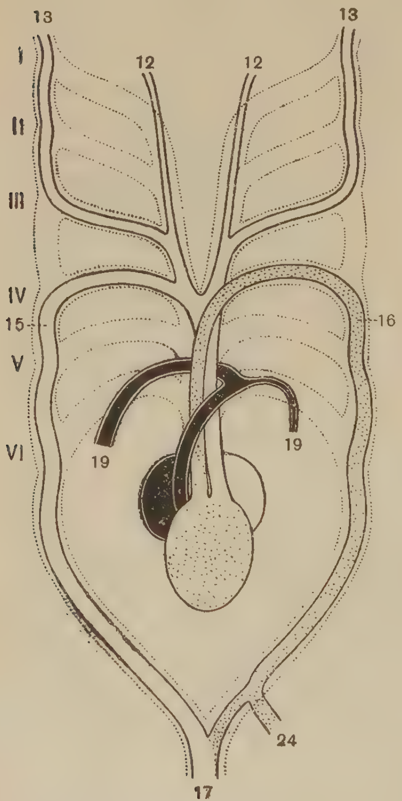

Fig. 291. Diagram of arterial arches of Snake viewed from the ventral aspect.

I, II, III, IV, V, VI. First to sixth arterial arches. 12. Tracheal (ventral carotid). 13. Common carotid (dorsal carotid). 15. Right systemic arch. 16. Left systemic arch. 17. Dorsal aorta. 19. Pulmonary. 24. Coeliac.

In the skull the chief point to be noticed is the extreme mobility of the jaws. The jugal as well as the quadratojugal have disappeared, the pterygoids no longer articulate with the base of the skull, and the quadrate itself is pushed away from the cranium by the squamosal[1], which is a rod-like bone (Fig. 290). The result of this arrangement is that when the lower jaw is pulled down, the quadrate is quite free to thrust the pterygoid forward and push up the maxilla by means of the transverse bone; that is to say there is the same mechanism as was described in the Lizard, only more easily set in motion and capable of much more movement. The halves of the mandible, or lower jaw, are connected by elastic fibres, and thus they can be widely separated. The result of this is that a Snake has an enormous gape and can swallow prey almost as large as itself. Snakes of quite moderate size dispose of frogs, birds, etc. The large Pythons of India can crush an animal larger than a half-grown sheep into a shapeless

[1] This so-called squamosal corresponds to the upper branch of the squamosal of *Lacerta*, and represents the tabular bone.

mass by coiling themselves around it, and they then swallow it whole.

The hyoid, including under that name the remains of all the hinder visceral arches, is vestigial, consisting of a single bone on each side. This permits of the pulling of the glottis far forward between the halves of the mandible when the animal is engaged in swallowing its prey, this shifting of position being necessary to prevent choking.

In the skull the brain extends forwards between the eyes and there is consequently no interorbital septum. That this is a secondary and not a primary state of affairs is shown by the fact that the front part of the brain is protected at the sides by downward extensions of the frontal and parietal bones, whereas the animals such as the Urodela and Mammalia, where an interorbital septum has never been formed, the side-walls of the cranium are constituted by the orbitosphenoid and alisphenoid bones. It is curious to find this absence of an interorbital septum in a family of limbless Lizards, the AMPHISBAENIDAE. What relation, if any, it has to the snake-like habits it is hard to guess.

The two eyelids have coalesced to form an extra guard in front of the eye, but there is a transparent portion in the lower one through which the animal can see. The outer covering of scales is shed periodically, half-a-dozen times every year or oftener, and replaced by a new set formed by the activity of the ectoderm, and during this process, since the covering of the eye is affected, the snake is blind.

One lung is small, and the other (the right) greatly elongated, the hinder part being quite smooth.

The heart resembles that of Lizards both in structure and the mode of distributing the arterial and venous blood. The differences between the vascular systems of a Snake and a Lizard depend chiefly on the absence of limbs and the correlated great development of the vertebral column, ribs and their musculature as organs of locomotion in the Snake. Thus the subclavian arteries are absent from the right systemic arch, while the vertebral and caudal arteries and veins are well developed. Another difference is that the left pulmonary artery is very slightly developed, in connection with the reduced condition of the left lung.

Snakes are divided into many families, of which two are represented in Great Britain and three in the temperate parts of North America. A rough classification would divide them according to their habits into: (*a*) those which poison their prey, (*b*) those which crush their prey, and (*c*) those which swallow their prey directly.

Those which crush their prey are confined to the tropics ; those which swallow their prey directly are the non-venomous snakes, and are represented in both England and North America by the family COLUBRIDAE. In this family the maxilla is long and bears numerous teeth, as do also the pterygoid and the lower jaw. The head is much broader behind than at the muzzle and passed into the trunk without any constriction to mark a neck. There are about thirty

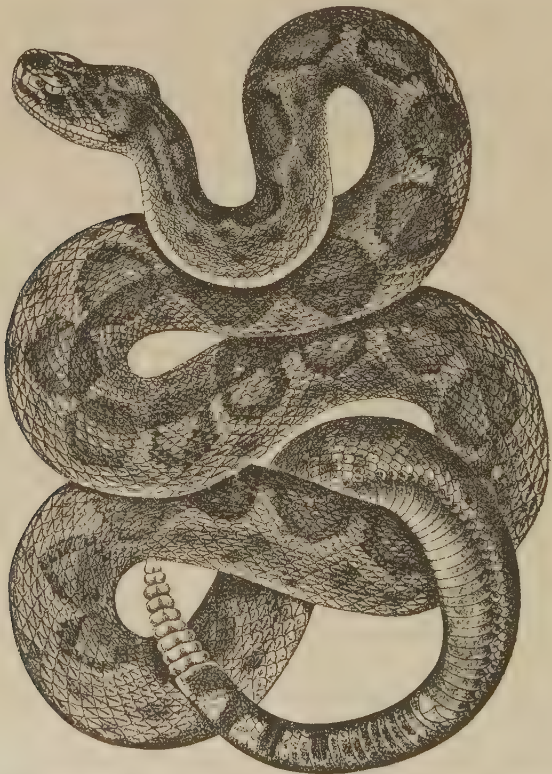

FIG. 292. The Texas Rattlesnake, *Crotalus atrox*, reduced. From Stejneger after Baird and Girard.

species belonging to eighteen genera in North America, of which *Tropidonotus* (*Eutainia*) *sirtalis*, the Garter-snake frequently met with in Canada, is one of the commonest; and in England the family is represented by two species, the Smooth-snake, *Coronella laevis*, and the Grass- or Ring-snake, *Tropidonotus natrix*.

The venomous Snakes in America belong to two families and these two families are not closely allied and have quite different

kinds of poison clearly indicating that the poison producing power has been independently evolved in different families of the Ophidia. In the first, the ELAPIDAE, the maxilla is a long bone and bears in front two large teeth which are grooved, to allow the secretion of glands in the lip to trickle down into the wound which they make. The poison acts directly on the nervous system of the victim paralysing the nerve centres which control respiration and heart action. The teeth behind are not grooved. The American Harlequin Snake, *Elaps fulvius,* belongs to this family. This Snake receives its name from its brilliant colours; it has seventeen crimson rings bordered with yellow. Another family is that of the VIPERIDAE. The maxilla is much shortened and bears one enormous fang, which when the mouth is closed lies against the roof of the mouth: when the mouth is opened the maxilla is rotated by means of the ectopterygoid, so as to erect the tooth. The poison in this family causes the blood of the victim to clot in its veins. The typical Rattlesnake—*Crotalus horridus* or *C. atrox*—derives its name from an appendage of about 8 to 9 loosely connected horny rings which it bears at the end of its tail, the shaking of which makes a noise like a rattle. This is one of the most deadly snakes known: it is found all over the United States in mountainous places and enters Canada. Like all CROTALINAE or Pit-vipers it has a sensory pit between eye and nose. The English Adder, *Vipera berus*, is, like all the Old World VIPERINAE, devoid of such pits. Speaking generally poisonous snakes may be recognised by their extremely swollen cheeks behind which there is a slightly narrowed neck, which passes into the trunk. The swelling of the cheek is due to the great enlargement of the poison-gland, which is a modified salivary gland (see p. 655) opening into the mouth.

Order III. **Chelonia.**

The Chelonia or Turtles are the most peculiar order of the Reptilia. In some respects they are nearest to the Amphibia, but they are highly specialised. Their leading peculiarity is the possession of two great shields, a dorsal—the carapace—and a ventral—the plastron, composed of bones firmly connected together, so that most of the organs of the body are enclosed in a box. The horny scales which cover in this box are very large and form what is known as tortoise-shell. The carapace is formed of a central row of neural plates which are expansions of the spines of the dorsal vertebrae with a nuchal plate in front of these and a pygal behind, the two last-named being of dermal origin.

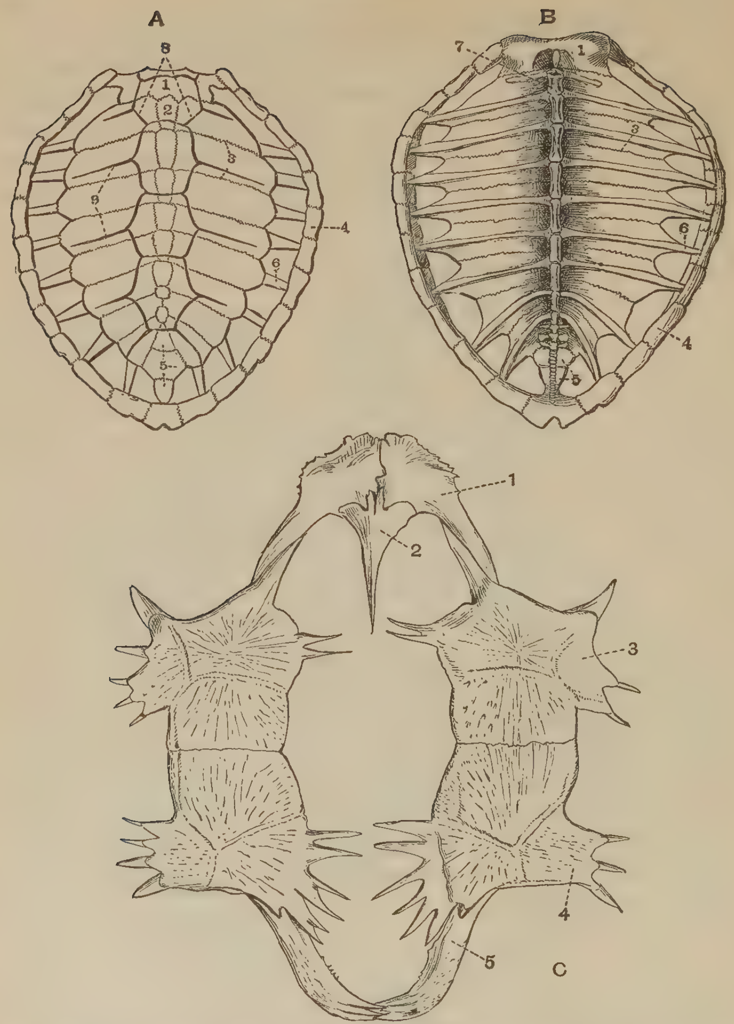

FIG. 293. A. dorsal and B. ventral view of the carapace of a Loggerhead Turtle, *Thalassochelys caretta*. After Owen. In A the outlines of the superficial horny scales constituting the tortoise-shell are indicated by heavy lines, whilst the outlines of the bones of which the carapace is composed are represented by lighter lines.

1. Nuchal plate. 2. First neural plate. 3. Second costal plate. 4. Marginal plate. 5. Pygal plate. 6. Rib. 7. Thoracic vertebra. 8. First vertebral shield. 9. Costal shield.

C. The Plastron of a Green Turtle, *Chelone mydas* $\times \frac{1}{7}$. (Camb. Mus.)

1. Epiplastron (clavicle). 2. Entoplastron (interclavicle). 3. Hyoplastron (cleithrum). 4. Hypoplastron. 5. Xiphiplastron.

On each side there are costal plates; this name is given to broad expansions of the outer surfaces of the ribs (Fig. 293). The ribs curve inwards to join the centrum, and since this, as in all Reptiles, is formed by the ventral intercalary, each rib is nearly opposite the interspace between two centra and sometimes unites

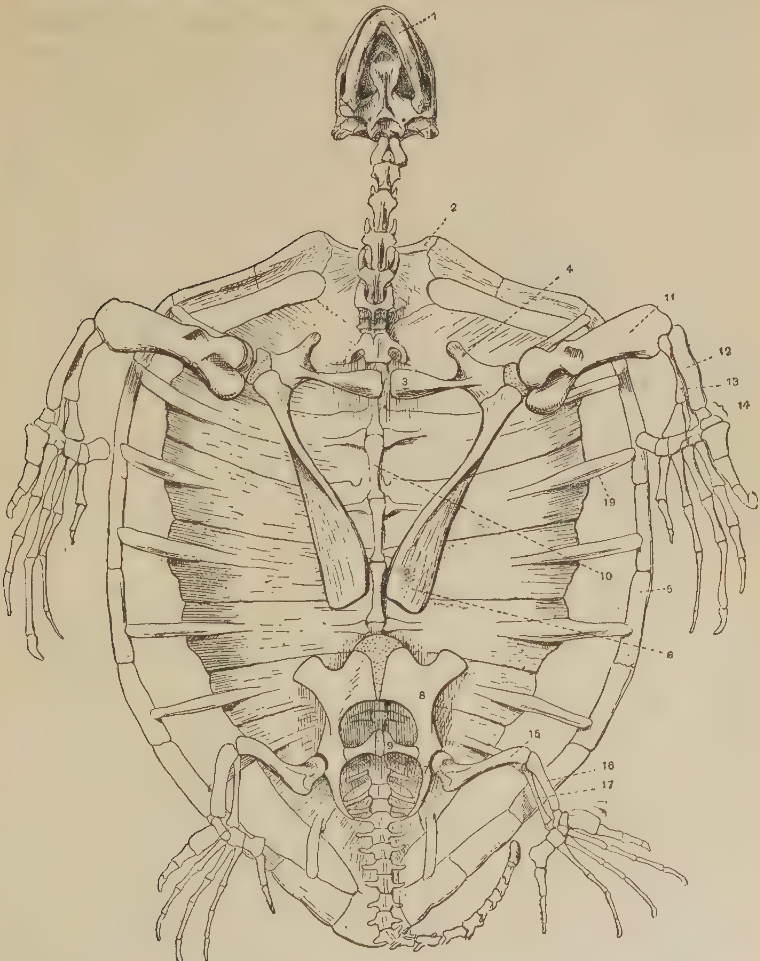

Fig. 294. Ventral view of the skeleton of *Chelone mydas*, the Green Turtle × about $\frac{1}{8}$. The plastron has been removed.

1. Lower jaw or mandible. 2. Nuchal plate. 3. Ventral process of scapula, the acromion. 4. Scapula (much foreshortened). 5. Marginal bone. 6. Coracoid. 7. Ilium. 8. Pubis. 9. Ischium. 10. Centrum of vertebra. 11. Humerus. 12. Radius. 13. Ulna. 14. Carpus. 15. Femur. 16. Tibia. 17. Fibula.

with them both. The transverse process is represented by the expansion of the neural plate which meets the costal plate. The almost horizontally directed outer ends of the ribs are received into a series of dermal bones called marginals, which form the edge of the carapace.

The plastron is formed of one unpaired and several paired bones (Fig. 293) The median bone, called the entoplastron, is believed to correspond to the interclavicle of other Reptiles. The first pair are called epiplastra and probably represent the clavicles of other forms. The posterior pairs are called hyoplastra, hypoplastra and xiphiplastra respectively; they are firmly joined to the marginals.

In front and behind the plastron and carapace are separated by soft flexible skin; their edges project so as to form roof and floor to cavities into which the head and neck and arms in front and the legs and tail behind can be withdrawn. A study of the development of modern Chelonia and of the anatomy of fossil species makes it probable that the ancestors of the present forms were provided with a carapace composed entirely of osteoderms underlying the horny scales, just as is the case with Crocodilia. This dermal carapace however was gradually replaced by the development of bony expansions of the ribs and neural arches; though remnants of it persist in the nuchal, pygal and marginal plates.

There is no trace of sternal ribs or sternum; but the pectoral and pelvic girdles occupy the peculiar position of being within instead of outside the ribs, a consequence of the almost horizontal direction of these. The girdles are in fact converted into pillars or struts which keep the plastron and carapace apart. In front the scapula forms a vertical pillar which has a ventral process—the acromion—projecting inwards beyond the articulation with the coracoid. This process is unique among recent Reptilia but existed in the extinct Plesiosauria. The coracoid slopes backwards and inwards. The ilium and pubis serve to support the carapace posteriorly. The pelvic girdle is similar to that of a Lizard but the pectoral girdle has no epicoracoid. The limbs are essentially similar to those of the Lizard but the toes are shorter and blunter. The neck is extraordinarily flexible; the vertebrae composing it fit one another by cup and ball joints, one is amphicoelous, the next is biconvex and so on. The dorsal vertebrae have flat faces.

The skull is devoid of teeth and the premaxilla and maxilla are short. Both they and the dentary have sharp cutting edges ensheathed in horn so as to form a beak. In all species the orbit is

encircled with a bony ring and the ectopterygoid or transverse bone is wanting. The palatal crest on the palatine is hardly perceptible. There is but one temporal arcade which is chiefly composed of jugal and quadratojugal bones. When the squamosal joins the postfrontal as it does in a few cases no fossa intervenes between this union and the jugal-quadratojugal bar. Chelonia as already explained are Monapsid reptiles and descended from a different stock from that which gave rise to the other groups of Reptiles. In the marine

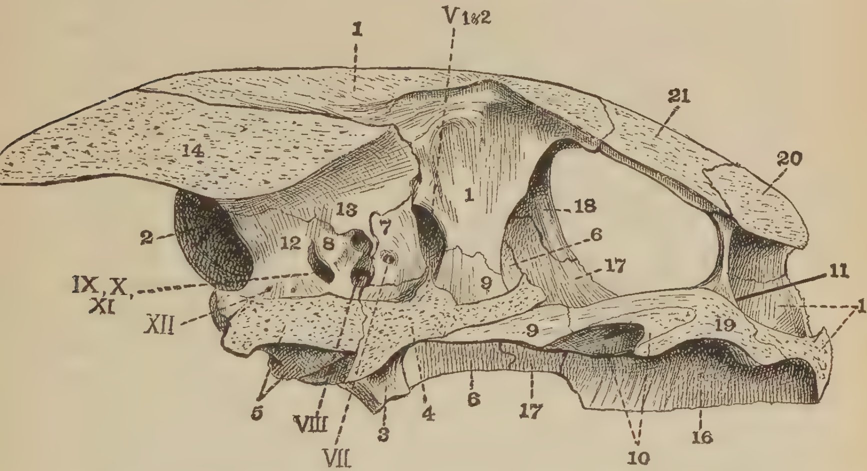

FIG. 295. Longitudinal vertical section through the cranium of a Green Turtle, *Chelone mydas* × ⅔.

1. Parietal. 2. Squamosal. 3. Quadrate. 4. Basisphenoid. 5. Basi-occipital. 6. Quadratojugal. 7. Pro-otic. 8. Opisthotic. 9. Pterygoid. 10. Palatine. 11. Rod passed into narial passage. 12. Exoccipital. 13. Epi-otic fused to supra-occipital. 14. Supra-occipital. 15. Pre-maxilla. 16. Maxilla. 17. Jugal. 18. Postfrontal. 19. Vomer. 20. Prefrontal. 21. Frontal. V 1 and 2, VII, VIII, IX, X, XI, XII. Foramina for the exit of cranial nerves.

Chelone and its allies the postfrontal, squamosal, parietal and quadratojugal coalesce to form a sheet of bone from the crest of the skull to the lip, roofing over a cavity lying at the side of the cranium and containing muscles. The parietals send downwards two vertical plates which meet upward extensions of the pterygoids.

Breathing is performed as in Amphibia, by a mylohyoid muscle and other muscles causing movements of the hinder visceral arches, of which there are three pairs.

The heart in structure and mode of action resembles that of Lizards and Snakes, the left-hand systemic arch conveying blood

chiefly venous to the viscera, while the right-hand one supplies the head, trunk and limbs with blood which is much more arterialised than that in the other arch (p. 581). The fore-limbs are however supplied by a different vessel from the subclavian of the Lizard. We have already seen (p. 451) that in some vertebrates the artery to the fore-limb arises from the systemic arch on its dorsal course to join its fellow, while in others the fore-limb receives its blood from an artery given off from the ventral end or commencement of the systemic arch or else from the ventral end of the third arch near its division into dorsal and ventral carotids. As the vessel to the fore-limb is always called a subclavian artery it is convenient to express the fact that this vessel is not homologous throughout the vertebrate groups by the terms "dorsal subclavian" and "ventral subclavian." In Amphibians and Lizards the subclavian is of the dorsal type, but in Chelonians and, as we shall see, in Crocodiles also, the arm is supplied by a ventral subclavian, a vessel which is homologous with the "scapular" artery to the shoulder muscles in a Lizard. The venous system in all chief respects is like that already described in the Lizard.

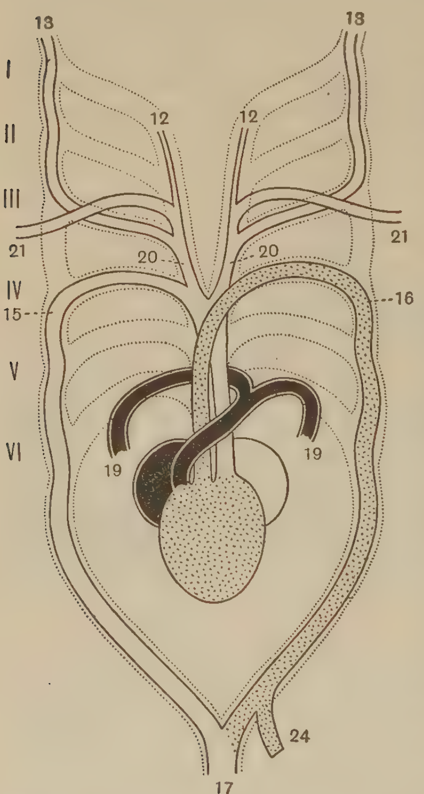

FIG. 296. Diagram of arterial arches of a Turtle viewed from ventral surface.

I, II, III, IV, V, VI. First to sixth arterial arches. 12. Tracheal (ventral carotid). 13. Common carotid (dorsal carotid). 15. Right systemic arch. 16. Left systemic arch. 17. Dorsal aorta. 19. Pulmonary. 20. Innominate. 21. Subclavian (ventral type). 24. Coeliac.

The copulatory organ is a grooved rod attached to the front

wall of the cloaca. The groove leads to the openings of the male ducts, the vasa deferentia.

The members of the order Chelonia have very various habits and modes of life. Some are vegetable feeders, others purely animal. None are found in Great Britain, but the representatives of six groups are found in temperate North America. These are

(1) The TESTUDINIDAE or Land Tortoises.
(2) The EMYDIDAE or Pond Turtles.
(3) The CINOSTERNIDAE or Box Turtles.
(4) The CHELYDRIDAE or Snapping Turtles
(5) The TRIONYCHIDAE or Mud Turtles.
(6) The CHELONIDAE or Marine Turtles.

The TESTUDINIDAE have a very arched carapace and short club-like limbs in which the toes are tightly bound together by skin. Only a few species, *Testudo polyphemus*, the burrowing Gopher, and *Cistudo carolina*, the Box Tortoise, are known in temperate North America.

The EMYDIDAE are represented by many species. In this family the carapace has a wide horizontal margin and the toes are connected by a web. Most of the species are aquatic, a few however are almost as terrestrial as the TESTUDINIDAE. *Chrysemys picta*, the Painted Pond Turtle, ranges north into the St Lawrence.

The CINOSTERNIDAE have a long and narrow carapace with the margins produced downwards; it is highest behind. The front part, and sometimes the hind part, of the plastron moves like a hinge on the rest and close in the head and tail, whence the name Box Turtle. Sole genus *Cinosternum*. *C. pennsylvanicum* is the most northerly species.

The CHELYDRIDAE are the so-called Alligator- or Snapping-Turtles. The head, neck and tail are all large and cannot be completely protected between the carapace and plastron. The carapace is highest in front. The jaws are hooked and powerful and the animals are very vicious. *Chelydra serpentina*, the "Snapper," is one of the commonest of American turtles. It is found everywhere from Canada to the tropics.

The TRIONYCHIDAE or Mud Turtles have no horny scales; both carapace and plastron are covered with leathery skin. There is a soft pig-like snout; only the three centre toes have claws. They seek their food by burrowing in the bottom of ponds.

The CHELONIDAE are distinguished by their peculiar skull and the absence of many or all of the nails. Their extremities have become flattened and form very efficient paddles.

Order IV. **Crocodilia.**

The last and highest order of the Reptilia is the Crocodilia. These animals agree with the Chelonia in having a series of osteoderms underlying the horny scales of the skin, also in having an immovable quadrate and a single median copulatory organ, but in spite of these resemblances, they seem to belong to the same stock

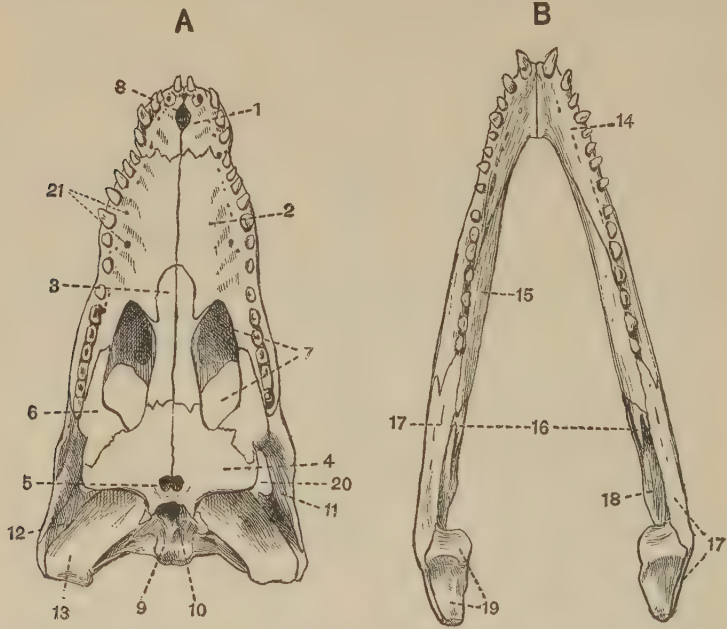

Fig. 297. Palatal aspect, A. of the cranium, B. of the mandible of an Alligator, *Caiman latirostris* × $\frac{1}{3}$.

1. Premaxilla. 2. Maxilla. 3. Palatine. 4. Pterygoid. 5. Posterior nares. 6. Transverse bone. 7. Posterior palatine vacuity. 8. Anterior palatine vacuity. 9. Basi-occipital. 10. Opening of median Eustachian canal. 11. Jugal. 12. Quadratojugal. 13. Quadrate. 14. Dentary. 15. Splenial. 16. Coronoid. 17. Supra-angular. 18. Angular. 19. Articular. 20. Lateral temporal fossa. 21. Openings for the passage of blood-vessels supplying the alveoli of the teeth.

as Sauria and Rhynchocephala; they are Diapsid not Monapsid in their skulls. It must be remembered that many families of Lizards possess osteoderms.

The Crocodiles are of large size and are decidedly Lizard-like in their general appearance, the chief observable external difference between them and the Lacertilia being in the jaws, which are

exceedingly long in comparison with the rest of the skull, so that the gape is very wide.

The osteoderms form rings on the tail, but on the body, as in Chelonia, they form a dorsal and a ventral shield separated by intervening softer skin. In many Crocodiles the ventral shield is very rudimentary.

In the general arrangement of the bones and the temporal fossae the skull resembles that of *Sphenodon*: but there are great differences in the jaws and palate. The maxilla is very long and is armed with conical teeth which are implanted in distinct sockets or alveoli, the bone having grown up round their bases.

The two palatal folds have met so as to completely divide the upper air passage from the lower food passage: both the palatines and the pterygoids being completely united in the middle line (Fig. 297). The choanae or posterior nares are therefore situated very far back directly over the glottis, whilst the external nostril is at the tip of the snout.

In consequence of this position of the external nostril the crocodile can lie for hours hidden under the water with only the tip of the snout exposed, and so surprise any unwary animal coming to the water to drink.

All the cervical and trunk vertebrae and some even of the caudal vertebrae bear ribs. The manner in which these ribs are articulated to the atlas and axis vertebrae throws much light on the relation of these peculiar vertebrae to the rest. Thus we observe that the first pair of ribs are articulated with their heads to the lower part of the atlas, showing that this represents a basiventral homologous with the intervertebral cartilaginous pads of the rest of the column. The heads of the second pair of ribs are united to an intervertebral cartilage separating the odontoid process from the centrum of the second vertebra. This cartilage is therefore the second basiventral, and the odontoid process is the first interventral, homologous with the centra of all succeeding vertebrae. The tubercle of each of the second pair of ribs has also an attachment to the odontoid process lying obliquely above and behind the capitular attachment and hence the centrum of the axis vertebra has no rib attached to it. The third pair of ribs have shifted their capitular attachment back on the centrum of the third vertebra (Fig. 298). This backward shifting of the capitular attachment has taken place in all succeeding vertebrae, and the head of the rib is attached directly under its tubercle. In the trunk, as we proceed

backwards, the capitular attachment to the centrum is gradually raised till it reaches the transverse process and is confounded with the tubercular attachment, and the hindermost vertebrae are single headed. There are abdominal ribs, as in *Sphenodon*; they are arranged in transverse rows, each row on each side consisting of three or four bones (Fig. 299).

The pectoral girdle consists of simply a scapula and coracoid, the latter reaching the sternum, which is cartilaginous but protected ventrally by an interclavicle (Fig. 300). In the fore-limb the carpus has retained three bones in the proximal row, but the distal row consists of a block of cartilage representing the first and second carpalia and a bone representing the remaining three. There is consequently an intercarpal wrist joint corresponding to the intertarsal joint common to Reptiles.

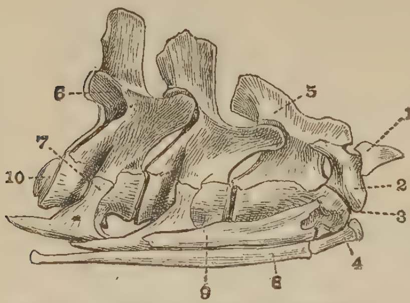

FIG. 298. First four cervical vertebrae of a Crocodile, *C. vulgaris*. Partly after von Zittel.

1. Neural spine of atlas. 2. Lateral portion of atlas. 3. Odontoid process. 4. Ventral portion of atlas. 5. Neural spine of axis. 6. Postzygapophysis of fourth vertebra. 7. Tubercular portion of fourth cervical rib. 8. First cervical rib. 9. Second cervical rib. 10. Convex posterior surface of centrum of fourth vertebra.

The pelvic girdle is very peculiar. The ilium is broad and rounded above and joins the two sacral vertebrae. The pubis does not form any part of the boundary of the acetabulum or socket for the head of the femur. This is completed by a small bone termed the acetabular bone. This exclusion of the pubis from the boundary of the acetabulum is a feature of modern Crocodiles, because in extinct Crocodiles the pubis took its proper share in forming the border of the acetabulum. The tarsus, like the carpus, is much reduced and modified. It consists of a proximal row of two bones, one of which, the fibulare or calcaneum, forms a distinct heel. The distal row consists of two bones, one representing the first, second and third tarsalia, the other the fourth and fifth.

The heart of the Crocodile is remarkable for the fact that the septum in the ventricle has grown forwards so as to completely divide it into two halves, the right and left ventricles. The left

root of the aorta arises from the right ventricle and crosses the right root, which arises from the left ventricle and gives off the two carotids. The left root therefore receives venous blood from the right auricle and the blood sent to the trunk is mixed. In addition there is a small passage, the foramen of Panizza, joining the two trunks where they cross, so that the blood leaving the right arch to go to the carotid is also somewhat mixed. The right common or dorsal carotid is very reduced, the left-hand vessel supplying both sides of the head (Fig. 301). The fore-limb receives blood by a subclavian of the ventral type, as in Chelonians. The lung is no longer a simple sac, but has thick spongy walls and the central passage is reduced to a narrow tube. In the brain the cerebellum is large and cylindrical.

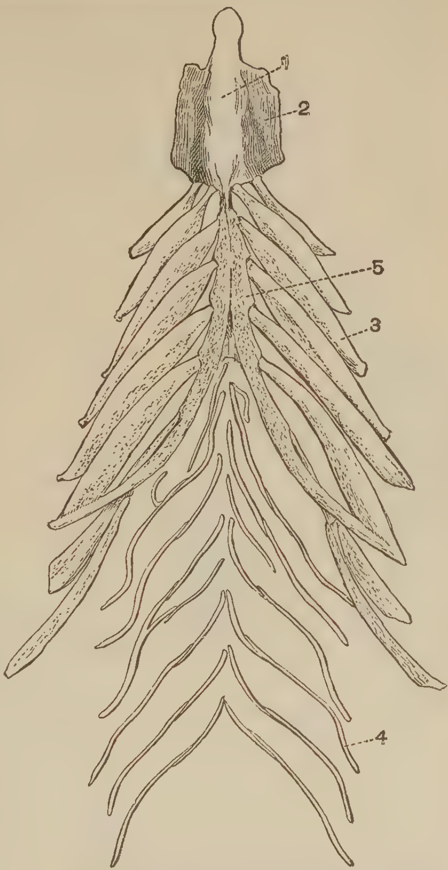

FIG. 299. Sternum and associated membrane bones of a Crocodile, *C. palustris* $\times \frac{1}{3}$.

The last pair of abdominal ribs which are united with the epipubes by a plate of cartilage have been omitted.

1. Interclavicle. 2. Sternum. 3. Sternal rib. 4. Abdominal splint rib. 5. Sternal band.

All these peculiarities of the internal organs may be termed foreshadowings of what is found in Birds and Mammals, and hence Crocodiles are styled rightly the highest of living Reptiles.

Crocodiles are inhabitants of rivers and swamps and spend most of their life in the water. The best known and classical example is the Crocodile of the Nile, *Crocodilus niloticus*. There is but one

species in the southern states of North America, the Alligator, *Alligator mississipiensis*, which has a much shorter and broader snout than the Crocodile. This animal lies for hours absolutely motionless at the surface of the water so as to greatly resemble a log, and thus entrap any unwary animal which may venture near. The Gavial, *Gavialis gangeticus*, in India is remarkable for its excessively long and narrow jaws.

So far as we can learn from fossils the Reptiles seem to have been the dominating type of land animals in the ages which inter-

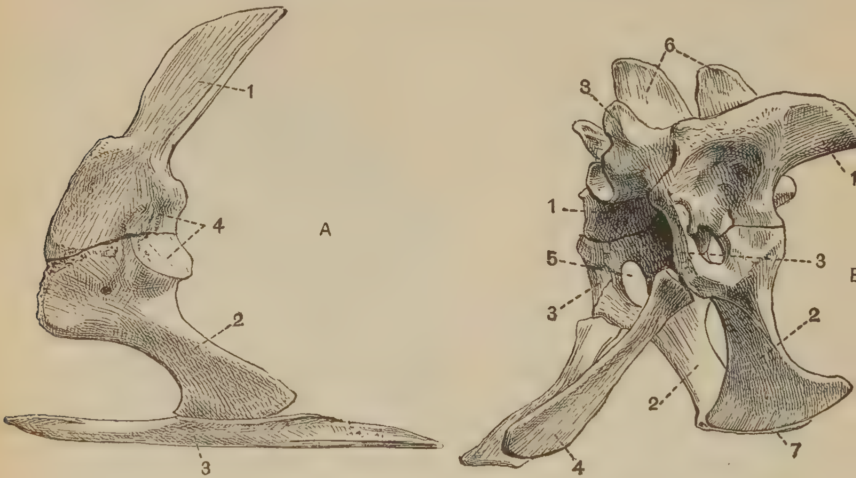

FIG. 300. A. Left half of the pectoral girdle of an Alligator, *Caiman latirostris* × $\frac{2}{3}$.

1. Scapula. 2. Coracoid. 3. Interclavicle. 4. Glenoid cavity.

B. Pelvis and sacrum of an Alligator, *Caiman latirostris* × $\frac{1}{2}$.

1. Ilium. 2. Ischium. 3. Acetabular bone. 4. Pubis. 5. Acetabular foramen. 6. Neural spines of sacral vertebrae. 7. Union of the two ischial bones. 8. Process bearing prezygapophysis.

vened between the close of the Coal epoch and the end of the Chalk period when the white limestone which constitutes the southern cliffs of Britain was deposited as a sediment in the quiet waters which covered what is now Western Europe. A rough sketch of the history of the class as deduced from fossils may be given here.

The Reptilia seem to have arisen from the most primitive forms included under the title Stegocephala. At least there are some forms like *Eryops* and *Cricotus* included in the latter group in which the bones flanking the notochord, which have not yet united so as to

form vertebrae, are represented by basidorsals, basiventrals, and ventral intercalary pieces, the dorsal intercalary piece as in all Reptilia being suppressed, while in the skull the basi-occipital region is ossified. In the Sandstones lying above the Coal indubitable Reptiles with fully formed vertebrae make their appearance. Some of these, termed the Cotylosauria, still recall the Stegocephala in possessing a complete roof of dermal bones covering the skull.

The descendants of the Cotylosauria in the next period split into two stocks, in one of these the Monapsida, the covering of dermal bones on the head was reduced in such a manner to leave one broad temporal bar.

The limbs in all these early Reptiles were short and stout, the fore- and hind-limbs being nearly of the same size. One group of the Monapsida, the Theromorpha, were distinguished by having the teeth differentiated into incisors, canines and molars and in having the dentary very large and articulating with the squamosal, the other bones of the lower jaw being reduced in size. These are almost certainly the ancestors of Mammalia.

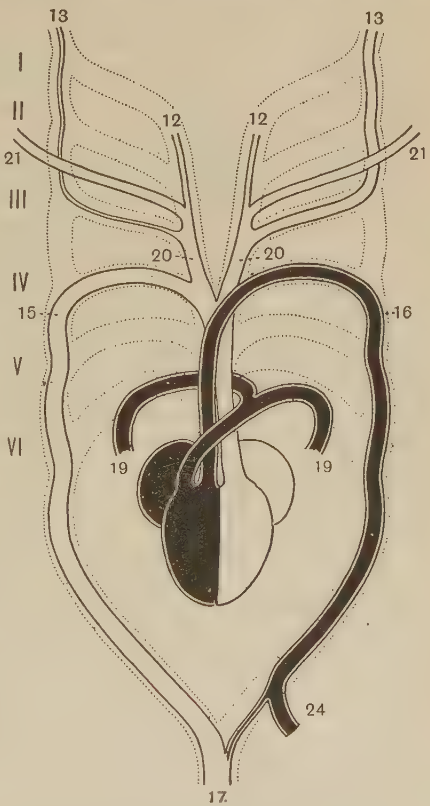

FIG. 301. Diagram of arterial arches of Crocodile viewed from the ventral aspect.

I, II, III, IV, V, VI. First to sixth arterial arches. 12. Tracheal (ventral carotid). 13. Common carotid (dorsal carotid) [right side nearly atrophied]. 15. Right systemic arch. 16. Left systemic arch. 17. Dorsal aorta. 19. Pulmonary. 20. Innominate. 21. Subclavian (ventral type). 24. Coeliac.

In another group of Monapsida the teeth were reduced to a pair of tusks in the upper jaw or were totally absent. This group

termed the Dicynodontia are believed by some to have been the forerunners of the Chelonia.

A third group of Monapsida was constituted by the great group of whale-like Reptiles known as Ichthyosauria in which the neck was absent and the limbs were transformed into flippers—the fingers being represented by long rows of squarish bones. The fingers frequently branched and supernumerary fingers were formed. Some exceptionally well preserved specimens show that the animals when alive possessed a dorsal fin.

The other division of the Cotylosaurian stem consisted of forms in which supratemporal and laterotemporal fossae were equally developed; these were the Diapsid Reptiles. The Rhynchocephala as represented by *Sphenodon* are almost unmodified survivors of the early Diapsida. From this group in the following age were developed (*a*) Water-Reptiles—the Plesiosauria—with long swan-like necks and limbs transformed into flippers by the shortening of the bones of the arm and leg, and (*b*) Land-Reptiles—the Dinosauria—with greatly developed limbs; in some cases the whole weight was borne by the hind-limbs, the fore-limbs being short and used for prehensile purposes only. In a still later period from the less specialised Dinosauria were developed (1) the Crocodilia, which reverted to the water but retained limbs fit for progression, and (2) Pterosauria, flying reptiles in which the "wing" was a flap of skin supported by the greatly elongated 5th finger. The forerunners of modern Sauria are found only in the Chalk period in the form of long-bodied aquatic Reptiles showing the characteristic loss of the quadratojugal.

The class Reptilia is classified as follows:

Order I. **Rhynchocephala.**

Reptilia devoid of special copulatory organs and with an immovable quadrate.

Ex. *Sphenodon.*

Order II. **Sauria.**

Reptilia with paired dorsal copulatory organs and a movable quadrate.

Sub-order 1. **Lacertilia.**

Sauria which retain a pectoral girdle and a urinary bladder; in which the rami of the lower jaw are united by a symphysis. Limbs present or absent.

Ex. *Lacerta, Anguis.*

Sub-order 2. **Ophidia.**

Sauria devoid of pectoral girdle and of urinary bladder; in which the rami of the lower jaw are united by an elastic ligament. Limbs absent.

Ex. *Crotalus, Vipera, Tropidonotus.*

Order III. **Chelonia.**

Reptilia with one median copulatory organ on the anterior wall of the cloaca and an immovable quadrate. No sternum and the ribs expanded horizontally to form a dorsal shield: a ventral shield of dermal bone. No teeth.

Ex. *Testudo, Chelone.*

Order IV. **Crocodilia.**

Reptilia with one median copulatory organ on the anterior wall of the cloaca and an immovable quadrate. A well-developed sternum, joined by the ribs. With many alveolar teeth.

Ex. *Crocodilus, Alligator, Gavialis.*

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CHAPTER XXIV

SUB-PHYLUM IV. CRANIATA

DIVISION II. GNATHOSTOMATA

SUB-DIVISION II. AMNIOTA

Class IV. AVES

General Characteristics.

IT is probable that if the first child one met were asked to describe a bird, he would say that birds were animals which were covered with feathers and had wings to fly with. Though it often happens that the marks by which the ordinary person distinguishes one animal from another are not those which seem most important to a zoologist, yet in this case the zoologist could not find more important features to serve as the basis of a definition of the class Aves or Birds.

Birds then are vertebrate animals in which the fore-limb is modified into a wing or flying organ and in which the body is covered with feathers. Bats likewise have the fore-limb converted into a wing, but they are covered with hair, not feathers, and their wing is not constructed on the same plan as that of the bird.

Birds are sometimes classed along with the Reptiles as Sauropsida, since they have a good many features in common with them, and are thus contrasted with the Mammalia, or ordinary quadrupeds. This, however, gives a wrong view of the relationships of the three groups. Both Birds and Mammals are believed to be descended from Reptilian-like ancestors, and it is an open question whether the changes which Birds have undergone are not at least as important as those which have taken place in Mammals in the process of their evolution from ancestors which, had they lived now, would have been termed Reptiles.

Birds agree with Reptiles in that they lay large eggs from which the young are hatched in a form closely resembling the parent; they are like Reptiles also in the structure of their jaws—the lower jaw consisting of five bones and articulating with a quadrate

bone—and in the structure of the hinder part of their skulls, of their breast-bones and of their ankle-joints. As in Reptiles, the number of neck vertebrae is variable. Like Reptiles, Birds have nuclei in the red corpuscles of the blood, and the sole remaining complete systemic arch goes to the right (Fig. 310), like the principal arch in Reptiles. On the other hand, they are "warm-blooded," that is to say, the temperature of the body remains practically the same whether the surrounding air gets hot or cold; it is in fact higher than that of any mammal: the ventricle of the heart is completely divided into two, and in addition to the wings and feathers, the structure of the leg and hip-bones and of the brain, distinguishes them from any living Reptile.

Feathers.

Strange as the statement may appear, it is true, nevertheless, that the feathers are really scales like those found in Lizards, but immensely developed and with the edges frayed out. Like scales, they are epidermal, that is, developments of the outer or horny layer of skin. The area which is about to form the feather becomes raised into a little finger-shaped knob by the growth of the deep layer of the skin or dermis which carries the blood-vessels. The little knob thus formed is in turn sunk in a pit called the follicle, the skin immediately surrounding it being depressed. Thus the lowest part of the feather is a little hollow tube of horny cells formed round the knob of dermis, but the upper part, like the scale of a lizard, is formed only on one side of the knob, and as this part is pushed away by the growth of the deeper parts it becomes frayed out so as to form the vane of the feather (Fig. 302). In the latter we can distinguish a central stem or rachis, and two rows of lateral branches or barbs, which are kept in position by a number of secondary processes or barbules. The barbules bear little hooks which interlock with one another. Down consists of small feathers growing between the bases of the larger ones. In these the barbules are absent, so that the barbs are not held together but float freely about, forming a kind of fluff. When a bird is plucked it is seen that the feathers are confined to certain tracts (pterylae) separated by others called apteria devoid of feathers or covered only with down feathers. Thus in most birds the mid-ventral and mid-dorsal lines are apteria. The colour of the feathers is partly due to coloured substances or pigments in the epidermal cells and partly to minute structural detail which causes interference of the light waves reflected from them.

The wing is the fore-leg of the bird. One can easily recognise the parts corresponding to upper arm, fore-arm and hand, but the latter is highly modified and specialised for the important function of carrying the long primaries or hand quills. When the wing is at rest the upper arm extends backwards, the fore-arm is sharply bent up on this, while the wrist is sharply bent down. When the wing is expanded these are partially, but never entirely, straightened out, so that a bird begins the down-stroke of the

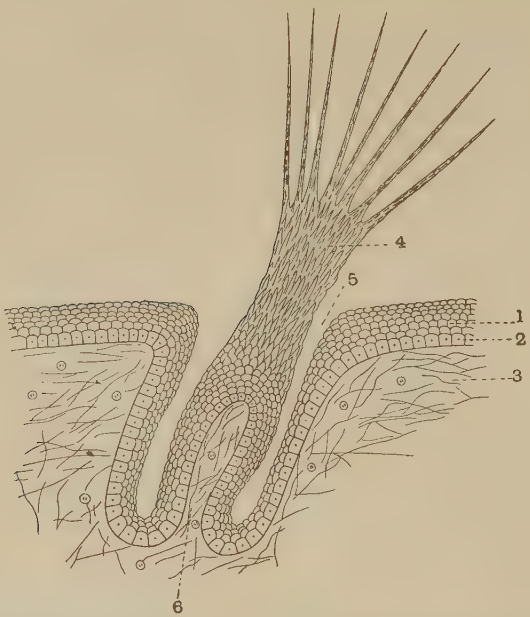

Fig. 302. Section through the skin of a Bird showing a developing feather. Highly magnified.

1. Epidermis. 2. Malpighian layer of the epidermis. 3. Dermis. 4. Young feather. 5. Follicle round base of feather. 6. Dermal papilla which develops blood-vessels and is the organ of nutrition of the feather.

wing with the arm bent in a very similar way to that in which a swimmer's arm is bent when he strikes back with it. In the hand we find as a rule three digits, the first, second and third. These have their first joints, the metacarpal bones, closely united together. In Man the metacarpals of the various fingers are united by skin and flesh which constitute the palm, but they are movable on one another, whereas in the bird the metacarpals of the

second and third digits are firmly joined at both ends. The index or second finger has in addition to the metacarpal, in most birds, three other small bones called phalanges, of which the end one sometimes carries a claw: the third digit has only one bone or phalanx besides the metacarpal. The metacarpal of the first digit or thumb is very small, but is likewise completely fused with the other metacarpals. Besides this the thumb has two joints and often a claw.

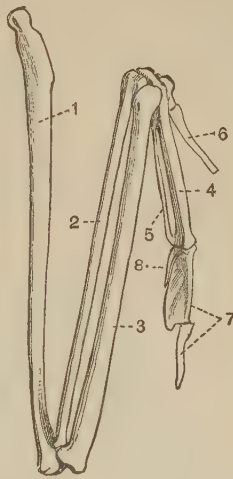

FIG. 303. Bones of the right wing of a Gannet, *Sula alba* × ½.

1. Humerus. 2. Radius. 3. Ulna. 4. Second metacarpal. 5. Third metacarpal. 6. Thumb or pollex. 7. Second digit. 8. Third digit. The distal phalanges of the thumb and second digit were wanting in the specimen from which this figure was drawn.

Compared with the arm or fore-leg of other animals the arm of a bird strikes one as having very little flesh. This is because the muscles, especially those on the fore-arm, have comparatively short bellies but very long tendons, in correlation with the often very much lengthened bones, one of which, the ulna, serves as support of the secondaries or arm-quills.

The movements which constitute flying, namely, the powerful down-stroke of the whole arm and the slower up-stroke, are carried out by the immensely developed pectoral muscles, great fleshy masses which cover the breast-bone or sternum. This bone has a more or less pear-shaped outline, rounded in front and pointed behind, the ribs ending in its sides (Fig. 304). In accordance with the tendency in all birds to develop the body into a long neck and a rounded trunk, we find evidence that the number of ribs encircling the body and joining the sternum has been reduced. Not only do we find small free ribs connected with the hinder cervical vertebrae, but attached to the sternum are outgrowths called costal and xiphoid processes (Fig. 304) which are regarded as the remains of sternal ribs the dorsal halves of which are vestigial or lost. If we picture to ourselves the pectoral girdle being thrust backwards and the pelvic girdle pushed forwards so as to crowd the viscera into a small space we shall realise the meaning of the differences between the skeleton of the trunk of a Reptile and that of a Bird, but it must not be supposed that the great length of a

bird's neck is a measure of the extent to which the pectoral girdle has been pushed back. From the relation of the cervical spinal nerves to the sympathetic ganglia it is certain that the greater part of the length of the neck must be regarded as due to a secondary zone of growth. From the middle of the sternum projects a great vertical crest stretching outwards, called the carina or keel, and it is from the sides of this mainly that the pectoral muscles take their origin. There are two main muscles on each side. First the pectoralis major on the surface, which passes into a tendon attached to the upper end of the humerus. The contraction of this muscle brings about the down-stroke of the wing, the effective stroke in flying. Underneath the pectoralis major is situated the pectoralis minor, a much smaller muscle. Its tendon passes underneath the arch formed by the clavicle and the coracoid bone, the latter of which, as in Reptiles, connects the shoulder-blade firmly with the sternum. Having passed through this arch which is termed the foramen triosseum because it is bounded by three bones, viz. clavicle, coracoid and scapula, the tendon is attached to the back of the humerus, so that the contraction of the muscle pulls the humerus and thus the wing upwards and backwards and not downwards, the upper end of the coracoid acting as a pulley round which it passes.

Fig. 304. Shoulder-girdle and sternum of Peacock, *Pavo cristatus* $\times \frac{3}{8}$.

1. Carina of the sternum. 2. Coracoid. 3. Scapula. 4. Clavicle. 5. Costal process. 6. Surfaces for articulation with the sternal ribs. 7. Posterior (xiphoid) and oblique processes.

Returning to the wing, we must now notice how the feathers are arranged. The great quill feathers are attached chiefly to the upper and posterior edge of the hand, but there are also a large number which are implanted in the posterior surface of the ulna. These two groups of feathers are pushed one over the other when the wing is folded, just like the silk of a closed umbrella, but when the wing is stretched out they only overlap very slightly, and thus a coherent and practically air-tight surface is formed. Those feathers which are attached to the hand are called primaries (6, Fig. 305, C), those

arising from the ulna, secondaries (8, Fig. 305, C); a few arising from the upper arm are called tertiaries; any air which might escape between the bases of the long feathers is stopped by an upper layer of shorter feathers, called coverts (1, 2, 3, 5 and 7, Fig. 305, C and D). Air is prevented from escaping in front by the hand, which is stretched out in a vertical plane, and by two folds of skin, one in the angle between fore-arm and upper arm, the other between the upper arm and the body. Each of these folds is termed a patagium. The name bastard wing is given to a tuft of feathers borne by the thumb (4, Fig. 305, C and D).

Flight.

The full mechanical explanation how the down-stroke of the wing not only prevents a bird from falling but urges it onwards is not completely understood, and much of what is generally accepted is too complicated for an elementary text-book, but the broad principles involved may be simply set forth. A bird when it is in the air, like any other heavy body, is continually falling: the blow of the wing has therefore not only to effect a forward impulse, but also an upward one sufficient to compensate for the distance the bird has fallen between two strokes. These impulses are derived from the elastic reaction of the air compressed by the down-stroke of the wing. When the wing is expanded, it is slightly convex above and concave beneath. This arises from the fact that the quill feathers are attached to the upper edge of the webbed limb and project gently downwards and backwards, so that there is a space left which is bounded behind by the quills and in front by the bones and the patagia. Now if this space had a symmetrical shape the air would be compressed in such a way that the resultant impulse would be directly upwards; but it is not symmetrical, for its roof has a very steep slope in front and a very gentle one behind, and the air is compressed in such a way that an oblique reaction results, a reaction which we can resolve by the parallelogram of forces into an upward and an onward one. So much for the flight of a bird in still air. The air is, however, very rarely still, and the currents which exist are never quite horizontal, but generally inclined slightly upwards, since the lowest layer of air is checked by friction against the ground, and birds which are good flyers can, by inclining their wings at the proper angle, obtain quite sufficient support from the play of the current against the wing without exerting themselves to any great extent. This is called soaring, and can be seen beautifully in the flight of the Gannet. In this

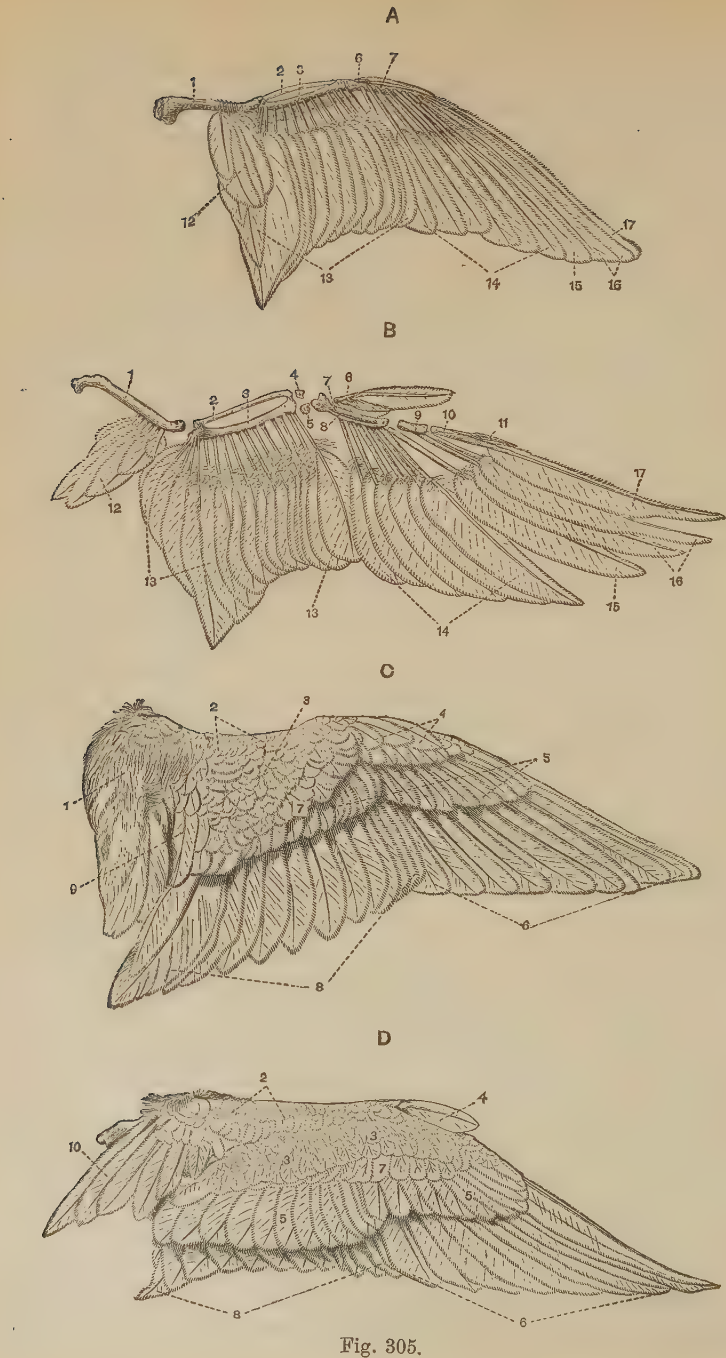
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Fig. 305.

FIG. 305. Wing of a Wild Duck, *Anas boschas* × ⅓.

A. Right wing seen from the dorsal side, with the coverts removed. B. Left wing disarticulated and seen from the ventral side, with the coverts removed. C. The dorsal side of a right wing. D. The ventral side of a left wing. From Wray.

In A and B. 1. Humerus. 2. Radius. 3. Ulna. 4. Radial carpal. 5. Ulna carpal. 6. First phalanx of first digit. 7. Second metacarpal. 8. Third metacarpal. 9. First phalanx of second digit. 10. Second phalanx of second digit. 11. Vestigial quill. 12. Tertiaries. 13. Secondaries. 14—17. Primaries.

In C and D. 1, 2, 3, 5, and 7. Coverts. 4. Bastard wing. 6. Primaries. 8. Secondaries. 9, 10. Tertiaries.

manœuvre birds are assisted by the tail, which is really a fan-shaped row of strong feathers attached to the coccyx, that very small vestige of a true tail or portion of the vertebral column extending behind the anus, which modern birds possess (Fig. 307). In this region the vertebrae are thin discs, several of which may be soldered together so as to form a bone called the pygostyle.

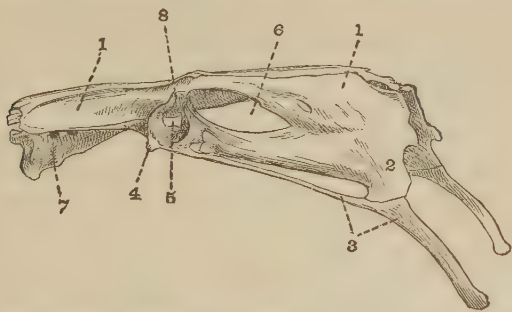

FIG. 306. Lateral view of the pelvis and sacrum of a Duck, *Anas boschas* × ⅔.

1. Ilium. 2. Ischium. 3. Pubis. 4. Pectineal process, the rudiment of the prepubis corresponding to the pubis of the Lizard. 5. Acetabulum. 6. Ilio-ischiatic foramen. 7. Fused vertebrae. 8. Facet on which the projection on the femur, the trochanter, plays.

Upright position.

The legs of birds can be shown to be constructed on essentially the same type as those of Reptiles, but modified so as to enable them to support the body in an upright position. The arrangements to effect this are very interesting, as they differ markedly from those found in the human skeleton. On the other hand they agree with the modifications of the hind limb found in those extinct Dinosauria which were bipedal.

In the pelvic girdle the ilia are lengthened so as to be attached to a considerable number of vertebrae, six or more, and so a firm attachment of the limb to the main skeleton is effected.

In Reptiles only two vertebrae are joined to the ilium, but in their case the weight of the body is supported on all four limbs, whereas in a Bird the whole vertebral column has to be balanced about two points of support, and hence the ilium must be quite immovably strapped to the vertebral column. The result of this has been atrophy of some of the hinder ribs, and the ventral halves of some of these form the xiphoid processes of the sternum. The ischium is directed backwards parallel to the hinder part of the ilium, and often fused with it so as to surround a space called the ilio-ischiatic foramen. The pubis is a very slender bone which is also directed backwards. It is in fact a postpubis corresponding to the lateral process on the pubis of the Lizard (see p. 577). Except in the Ostrich the two pubes never unite with one another ventrally to the cloaca, as they do in Reptiles and Mammals, the absence of a pubic symphysis facilitating the laying of the egg, which is very large relatively to the size of the animal. The thigh is bent sharply forwards and the shank backwards, and the ankle is raised to a considerable height above the ground by the great length and upward direction of the bones of the sole or metatarsals (Fig. 307). Thus a Bird walks on its toes and like Reptiles possesses an intertarsal ankle-joint. In Birds however, in order to give firmness to the leg, the metatarsals are closely united together and the small bones of the tarsus have entirely disappeared, the proximal row having been incorporated with the tibia, while the distal bones have fused with the metatarsals. Thus in an adult Bird the ankle-joint is a simple hinge between two compact bones, the upper being a tibio-tarsus, the lower a tarso-metatarsus. There are usually four toes, but the first, corresponding to the human great toe, is sometimes absent, while its metatarsal remains distinct from the other three. This toe, except in Steganopoda, is directed backwards. In the Parrot the fourth toe is also directed backwards. In the Cuckoo the fourth toe is directed backwards but can be turned forwards at will. In swimming and diving birds the second, third and fourth toes are generally connected by a web of skin. Only in Steganopoda is the hallux included in this web and in these birds this toe is turned forwards like the rest. In other swimming and diving birds the hallux is either absent or when present is free from the web and turned backwards. The raised sole of the foot really constitutes the visible "leg" of most birds, the thigh being altogether, and the shank mostly, buried in the feathers. In many birds the sole is

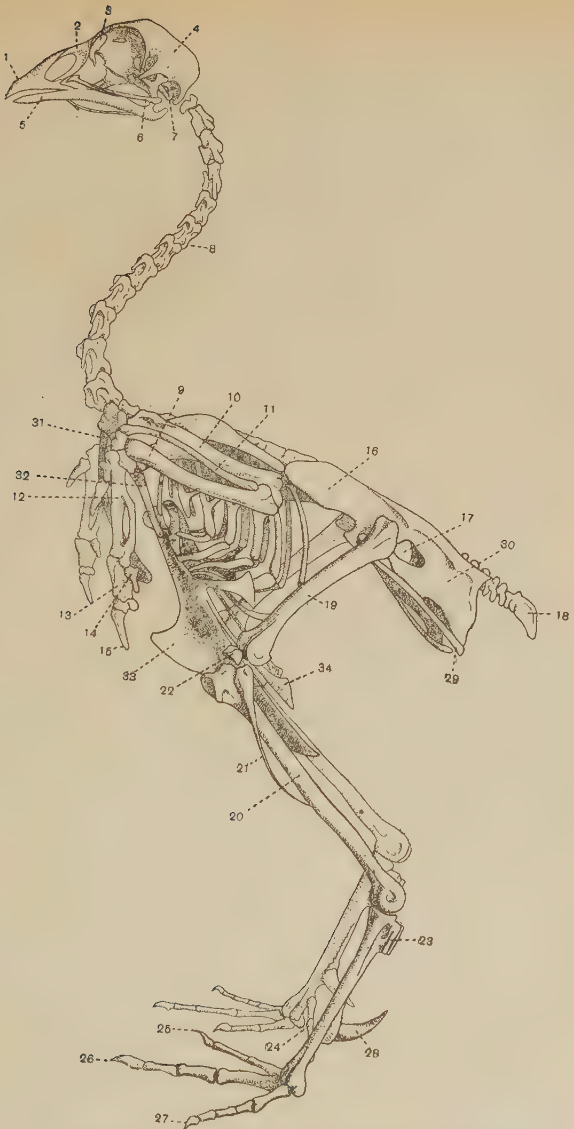

FIG. 307. Skeleton of the Common Fowl, ♂, *Gallus bankiva* ×½.

1. Premaxilla. 2. Nasal. 3. Lachrymal. 4. Frontal. 5. Mandible. 6. Lower temporal arcade in region of quadratojugal. 7. Tympanic cavity. 8. Cervical vertebrae. 9. Ulna. 10. Humerus. 11. Radius. 12. Carpometacarpus. 13. First phalanx of second digit. 14. Third digit. 15. Second digit. 16. Ilium. 17. Ilio-ischiatic foramen. 18. Pygostyle. 19. Femur. 20. Tibiotarsus. 21. Fibula. 22. Patella. 23. Tarso-metatarsus. 24. First toe. 25. Second toe. 26. Third toe. 27. Fourth toe. 28. Spur. 29. Pubis. 30. Ischium. 31. Clavicle. 32. Coracoid. 33. Keel of sternum. 34. Xiphoid process. The forked bone just in front of 7 is the quadrate.

plated by scales which are raised horny plates of skin, similar to the scales of Reptiles. The fifth toe corresponding to the little toe of the human foot is always absent.

Head and Neck.

The most characteristic features about a bird, next to the limbs and feathers, are certainly the head and neck. The skull is high and arched behind in order to make room for the comparatively large brain; in front it slopes gradually downwards to the pointed beak, which is encased in a hard horny sheath. The bones which underlie this beak are (above) the premaxilla and (below) the dentary bone of the lower jaw. No modern bird possesses teeth, and the maxilla, which usually carries most of the teeth in animals which have them, is very small and confined to the cheek behind the gape, whereas the premaxilla is very large. Behind the maxilla two other slender bones, the jugal and quadratojugal, complete the lower temporal arcade as in Chelonia and Crocodilia, but the jugal never sends up a process behind the orbit and the postorbital is a mere process of the frontal bone, so that the orbit and the temporal fossa open into one another. The eyes are of great size: a bird has little or no sense of smell, and governs its life mainly by the sense of sight: in correspondence with this the orbits or eye-sockets are so enlarged that the skull between them is reduced to a thin vertical plate, the interorbital septum, in which there is no brain cavity. This great development of the eye-sockets and the obliteration of the brain cavity between them is not, however, confined to Birds: it is found as already mentioned in many Reptiles also, and is indeed one of the several points in which a bird's skull may be said to be Reptilian. It is however characteristic of Birds, as opposed to Reptiles, that this interorbital septum is largely converted into bone. In its hinder and upper portions it is composed of orbitosphenoid bones, like those found in Teleostean fishes, which support the exit of the optic nerve, but in its lower part it is composed of a vertically compressed presphenoid bone corresponding to that which ossifies the front part of the floor of the cranium in Mammalia. In front the interorbital septum is continuous with the internasal or ethmoid septum: this latter is ossified by a mesethmoid bone, which unites, but not quite immovably, with the presphenoid. The hinder part of the floor of the cranium is ossified by the basioccipital and basisphenoid bones, and the front of the latter is drawn out into a long spur called the basisphenoidal rostrum. Underlying the basisphenoid there is a membrane bone called the

basitemporal, a relic of the parasphenoid of Fishes and Amphibians. In some Reptiles traces of the front part of this bone remain, but in no living Reptile does any trace of the hinder portion of the bone persist, and this is an indication that Birds are descended from a type of Reptile more primitive in some respects than any now existing. Other points of resemblance to Reptiles are that the lower jaw is ensheathed by five dermal bones and has its proximal end replaced by a cartilage bone, the articular; and that instead of there being a direct hinging or articulation of the lower jaw to the skull, a bone called the quadrate is interposed,

Fig. 308. Brain of Pigeon, *Columba livia* × about 2.

1. Olfactory lobes. 2. Cerebral hemispheres. 3. Pineal gland. 4. Optic lobes. 4a. Optic chiasma. 5. Cerebellum. 6. Lateral lobe of cerebellum. II. Optic nerves. III. Motor oculi. IV. Patheticus. V. Trigeminal. VI. Abducens. VII. Facial. VIII. Auditory. IX. Glossopharyngeal. X. Vagus. XI. Spinal accessory. XII. Hypoglossal.

as in Reptiles, which articulates on the one hand with the lower jaw and on the other with the skull. This quadrate bone is movable, and to it in front are jointed the bones of the palate, the pterygoids and palatines, which slide on, but are not fixed to, the base of the skull. Hence when the lower jaw is opened, i.e. pulled down, these bones are pushed forward, and the upper beak, to which they are fastened in front, is slightly tilted up, thus increasing the width of the gape. In parrots the front part of the skull, including the bones of the face, has an actual joint with the hinder part of the skull. Thus it follows that in spite of the presence of a quadratojugal

the quadrate is movable. It is to be remembered however that the quadratojugal is here a small flexible bone, very unlike the great bony bar of Chelonia and Crocodilia. When a bony palate is developed this is produced not by the union of outgrowths from the palatine bones as in Crocodiles (and we may add as in Mammals), but by outgrowths from the maxillary bones termed maxillo-palatines which extend inwards towards the middle line dorsal to the palatines. The hyoid apparatus consists of the second and third pairs of visceral arches. The second pair, which correspond to the hyoid of Fishes, are very short and consist mainly of the median piece or glossohyal which is closely connected to the median piece of the third pair. The latter are elongated rods to which are attached the muscles which protrude the tongue. As in the Reptilia, the skull has one central knob or condyle for articulation with the backbone, not two, as is the case with the Amphibia and Mammalia.

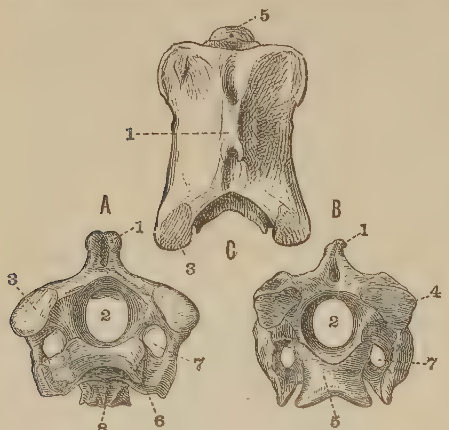

FIG. 309. Third cervical vertebra of an Ostrich, *Struthio camelus* × 1. A, anterior, B, posterior, C, dorsal view. A and B after Mivart.

1. Neural spine. 2. Neural canal. 3. Prezygapophysis. 4. Postzygapophysis. 5. Posterior articular surface of centrum. 6. Anterior articular surface of centrum. 7. Canal between the capitulum and tuberculum of the rudimentary rib. 8. Hypopophysis, a median ventral outgrowth of centrum.

The features peculiar to the Bird are, firstly, the great elongation of the premaxilla carrying the beak—this causes the nostrils to be placed at the base of the snout instead of at the tip, as is the case with most modern Reptiles, but a great many extinct Reptiles agreed in this respect with Birds; secondly, the enormous size of the orbit and the absence of any bony bar to separate it from the temporal fossa, the hollow on the side of the skull, in which are situated the muscles that close the jaws; and thirdly, the height and arched character of the hinder part of the skull, which lodges the brain. The bones of the skull are usually indistinguishably united in the adult, are hollow and contain air, and are in consequence very light,

as befits an animal which flies. Similar air spaces also exist in the larger bones of the trunk and limbs. The insects, which also have taken to the air, have somewhat analogous air reservoirs. Like insects, birds are represented by a large number of species which all exhibit great uniformity of structure.

The Brain.

When the brain is examined, the meaning of many of the peculiarities of the skull is seen. What we might perhaps, with a little looseness, call the organs of thought, the hemispheres of the fore-brain, are greatly enlarged, being high and rounded, but sections reveal the fact that the great mass of the hemisphere is composed of an enlargement of the base which corresponds to what is called corpus striatum in the mammalian brain. The roof of the hemisphere corresponding to the cortex in Mammalia is thin. Now in Mammals the corpus striatum is generally regarded as the seat of those impulses which carry out the instinctive activities, whereas the cortex is the seat of purposive action. In accordance with their brain-structure, we find that Birds are creatures of instinctive impulse, and have not nearly so much intelligence as they are usually credited with by imaginative people. One instance may suffice. The cuckoo nestling forces its foster parents to feed it by uttering a peculiarly plaintive cry. The impulse to provide the food is a mechanical reaction to this cry, for if the foster parents be shot, the cuckoo nestling will arrest the flight of other parent birds on their way to their nests and cause them to neglect their own young and feed the voracious cuckoo till they sometimes drop dead of exhaustion. The parts of the brain supplying the nose, the olfactory lobes, are very small and poorly developed, in accordance with the feebly-developed nasal sacs, the sense of smell being but slight, as mentioned above (Fig. 308). The brain is bent sharply on itself, so that the optic lobes of the mid-brain—portions connected largely with vision—are pressed downwards and the hemispheres are brought close to the cerebellum, which, in contradistinction to what is the case in most reptiles, is large and transversely wrinkled. Evidence is accumulating that an important function of the cerebellum is to coordinate the motor impulses to the skeletal muscles which bring about the correct balance of the animal. As balance is a more difficult matter in a bipedal animal than in a quadruped the cerebellum of birds is correspondingly enlarged.

All Birds have comparatively long necks (Fig. 307), and the vertebrae which form the support of this part of the body have the surfaces with which they articulate with one another shaped like

saddles, being concave from side to side and convex from above downwards in front and exactly the opposite curvatures behind (Fig. 309). This arrangement allows great freedom of movement, and the head and flexible neck of a bird may be said to play the part which hand and arm play in human economy. The fore-limb of Birds, from its function as a wing, is rendered totally useless for prehension. As all know, a Bird is able to twist the head completely round and look straight backwards. In doing so, of course it squeezes the skin of one side of the neck and stretches that of the other, and so the great jugular vein, which carries blood from the head, is liable to be blocked on one side (Fig. 311). To obviate this difficulty, the two jugulars are connected by a cross piece just under the head, so that the blood from both sides can always have a free passage. The carotid arteries, which take blood to the head, come close together at the base of the neck and run up just under the vertebrae. As they are placed close to the axis of rotation and are further protected by curved rods growing out from the vertebrae and forming arches over them, they are never compressed, however much the bird twists its neck.

Vascular System.

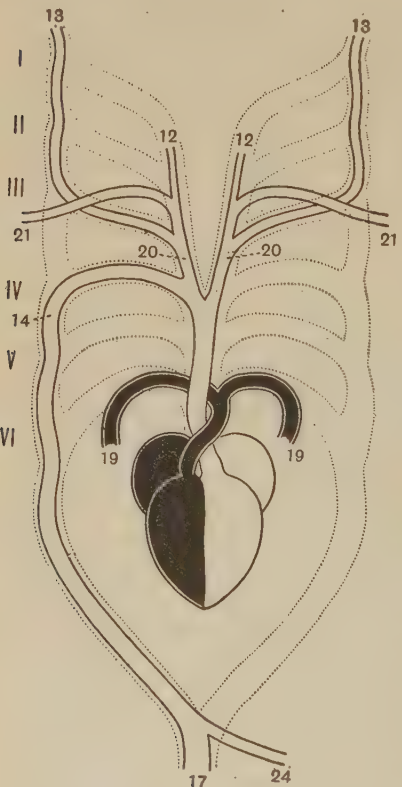

FIG. 310. Diagram of arterial arches of a Bird viewed from the ventral aspect.

I, II, III, IV, V, VI. First to sixth arterial arches. 12. Tracheal (ventral carotid). 13. Common carotid (dorsal carotid). 14. Systemic arch. 17. Dorsal aorta. 19. Pulmonary. 20. Innominate. 21. Subclavian (ventral type). 24. Coeliac.

Turning now to the consideration of the internal organs, we have first to notice the structure of the heart. In Birds the ventricle is completely divided into two, a condition found only in the Crocodiles among Reptiles, and even there the

great trunks leaving the two parts of the ventricle communicate. In Birds only one systemic arch remains complete; this passes round to the right, coming off from the left half of the ventricle; in Reptiles, it will be recollected, the left fellow of this one was still present. From the systemic arch there arises an innominate artery for either side, supplying the trachea, which splits up into a ventral carotid, as in Reptiles, but reduced as compared with the corresponding vessel in them, and into a dorsal or common carotid which supplies the head and a subclavian which supplies the breast and wing. The subclavian artery which arises from the ventral carotid divides into a brachial artery of moderate size for the wing and a very much larger pectoral artery which supplies the pectoral muscles. These, as we have seen, are the real seat of the activities of the wing. The subclavian of Birds corresponds in origin with that of Chelonians and Crocodiles and so is the ventral type of subclavian, as opposed to the dorsal type found in Lizards and Amphibians. The arteries supplying the lungs, the pulmonaries, which, as in the Reptiles, have no longer any connection with the systemic arch, come off from the right side of the heart; one passes to each side to reach the lungs (Fig. 310). The arteries of the hinder part of the trunk agree in their general arrangement with those of Reptilia and Amphibia. In the venous system the connection of the two jugulars has been already referred to. The jugular joins a large subclavian vein to form the superior vena cava. The largest part of the subclavian vein, like that of the corresponding artery, is made up of a pectoral vein returning blood from the pectoral muscles. The front parts of

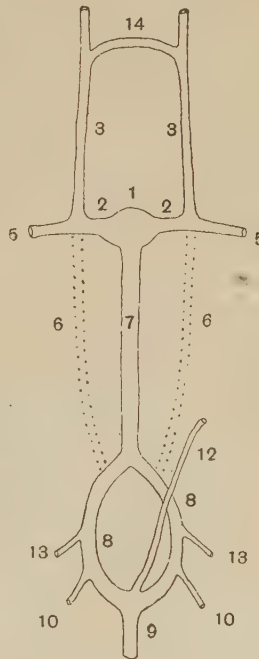

Fig. 311. Diagram to show arrangement of the principal veins of a Bird.

1. Sinus venosus—gradually disappearing in the higher forms. 2. Ductus Cuvieri = superior vena cava. 3. Internal jugular = anterior cardinal vein. 5. Subclavian. 6. Posterior cardinal, front part. 7. Inferior vena cava. 8. Renal portal = hinder part of posterior cardinal. 9. Caudal. 10. Sciatic. 12. Coccygeomesenteric. 13. Femoral. 14. Anastomosis of jugulars.

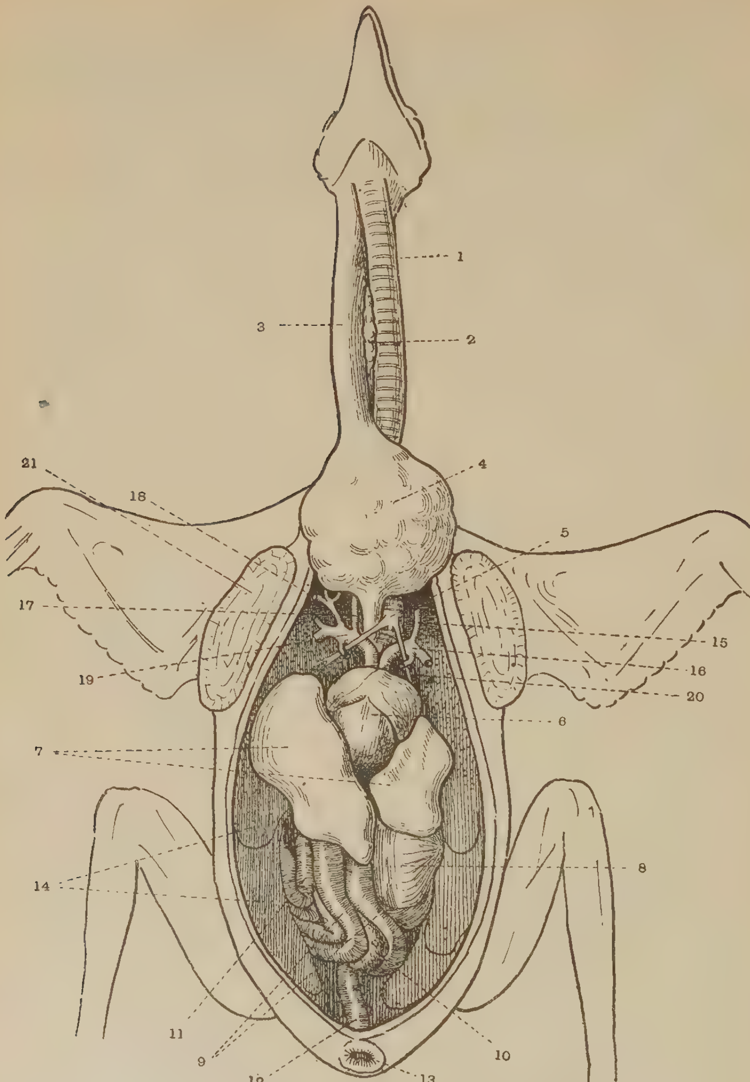

FIG. 312. The chief viscera of the Pigeon, *Columba livia* × ⅔.

1. Trachea. 2. Thymus gland. 3. Oesophagus. 4. Crop. 5. Syrinx. 6. Heart. 7. Liver. 8. Gizzard. 9. Duodenum. 10. Pancreas. 11. Small intestine. 12. Rectum. 13. Cloaca. 14. Air-sacs. 15. Left carotid. 16. Left subclavian. 17. Right carotid. 18. Brachial artery. 19. Right subclavian. 20. Muscles of syrinx. 21. Pectoralis major muscle cut across.

the posterior cardinal veins have disappeared: but their hinder parts remain as the renal portal veins which as usual arise by the bifurcation of the caudal vein and receive on each side a femoral and a sciatic vein from the leg. The renal portal pours its blood into the inferior vena cava, not as in Amphibia and Reptiles through a system of capillaries, but directly by a single vessel channelled through the substance of the kidney. Hence in Birds the kidney tubules receive blood only from the aorta and do not, as in the lower Craniata, receive a double supply. From the point where the caudal vein divides into the two renal portals a vein is given off which descends into the mesentery and opens into the posterior mesenteric branch of the portal vein, thus establishing a connection between the portal and cardinal systems of veins. This vein is called the coccygeomesenteric (12, Fig. 311), and is quite peculiar to Birds.

Respiratory System.

The lungs are firmly fitted in against the ribs; they do not, as in most Reptiles or as in ourselves, hang freely in a cavity; their most remarkable feature is the possession of great thin-walled bladder-shaped outgrowths, the air-sacs, of which the prolongations extend even into the bones. There are nine of these great air-sacs, one placed at the base of the neck, and the other eight situated in pairs at the sides of the body cavity under the ribs (Fig. 312). When the ribs are in their normal position, the air-sacs are expanded, but when the ribs are pulled backwards so as to compress the air-sacs, air is driven out; when the ribs and wall of the body behind come into their natural position again, the air-sacs are expanded and air rushes in. Breathing out or expiration is therefore the active function drawing in air is an elastic reaction, the opposite to what is the case in Man and other Mammals. It must be remembered that in the lungs of Birds as indeed of those of all other land animals the air which is breathed in or out, the tidal air as it is termed, is only a fraction of the total air contained in the lung. Oxygen and other gases pass from the tidal air to the residual air and *vice versâ* by the swift process of gaseous diffusion and as the torrent of tidal air rushes past the lungs into the air-sacs the lungs abstract oxygen from it, both on its way in and on its way out. This double oxygenation of the air in each complete set of respiratory movements is perhaps the reason for the extraordinary activity and strength of Birds in proportion to their size.

The windpipe or trachea is long, and the hoops of cartilage

which stiffen it form complete rings, so that it is not easily compressed (Fig. 312). Like most other land vertebrates, birds have a larynx or organ of voice at the top of the trachea formed in the usual manner by the enlargement of some of these rings of cartilage, and the stretching of a thin membrane between them and two special cartilages, the arytenoids, which lie at the opening of the windpipe into the gullet. The larynx however appears to be functionless, and the effective organ of voice in Birds, the syrinx, is found much deeper down, at the spot, namely, where the windpipe splits into two tubes, the bronchi, which lead to the lungs. The last rings surrounding the trachea just before it bifurcates are more or less fused with their successors and predecessors so as to form a box with stiff walls called the tympanum. The inner walls of the bronchi, just where they join one another, are thin and membranous, and constitute a membrana tympaniformis interna. From the fork a flexible valve, termed the membrana semilunaris, projects up into the tympanum, and as here the cartilage rings have the form of half-hoops, which are drawn together by special muscles, the width of the opening of the bronchus into the windpipe is small. When air is forcibly expelled the valve above mentioned is set vibrating like the reed in an organ-pipe, and by this mechanism the song is produced. The muscles which connect the half-rings together (intrinsic muscles) and two which connect the syrinx with the sternum (extrinsic muscles) by altering the tension of the sides of the trachea, and consequently the rate at which it vibrates, change the pitch of the note produced. A syrinx such as we have described is found in the vast majority of birds. It is termed a broncho-tracheal syrinx because both bronchi and trachea are concerned in its formation. In a few North American birds a tracheal syrinx is found in which the organ of voice is constituted by a portion of the trachea where the rings are thin and delicate, so that the sides are flexible. In a few birds allied to the Cuckoo there is a bronchial syrinx, a thin flexible membrane being formed about the middle of each bronchus by the incompleteness of some of the rings.

Digestive System.

The alimentary canal commences with the buccal cavity or stomodaeum, partially divided by the palatal flaps into an upper air-passage, and a lower food-passage. The flaps as we have seen are stiffened by the maxillopalatines. The tongue, which is pointed and horny, ensheaths the glossohyal bone; it is protruded by the action of muscles

which pull the enlarged third visceral arch forwards. Behind the tongue open the ducts of the submaxillary glands; at the corners of the gape the parotid glands pour their secretion into the mouth, whilst at the sides of the tongue the sublingual glands open. All these glands are pouch-like outgrowths of the ectoderm of the stomodaeum and secrete a mucus which assists in swallowing the food, and occasionally (as in Woodpeckers) in causing the prey to adhere to the tongue. The names indicate the position of the glands, as for instance, parotid (Gr. παρά, beside, οὖς, ὠτός, the ear). Following on the buccal cavity and indistinguishably fused with it is the endodermal pharynx into which the glottis opens, and also the persistent remains of the first pair of gill-sacs, the Eustachian tubes. The pharynx leads into a long gullet lying dorsal to the trachea, which eventually passes into the stomach. The gullet in the Pigeon and many other birds develops a large thin-walled outgrowth on the ventral side called the crop. This is used as a storehouse for the food, and in the Pigeon may be found full of unaltered seeds. The stomach has a most characteristic form in Birds; it is sharply divided into two regions, an anterior egg-shaped one called the proventriculus, and a large posterior flattened one called the gizzard. In the walls of the proventriculus are found the pepsin-forming glands, while on the other hand the endoderm of the gizzard develops a horny lining which is thin in Birds that live on an animal diet, but very thick in a grain-eating Bird like the Pigeon, where it forms upper and lower hardened plates. When by the contraction of the greatly thickened visceral muscles of this part of the alimentary canal the upper and lower plates are brought together, a crushing-mill is produced by which the food is broken up. The action of this mill is assisted by the habit which many Birds possess of swallowing fragments of stone. A collection of these, sometimes including fragments of glass, may be found on opening the gizzard of a Pigeon. It is a great development of this habit which has earned for the Ostrich its reputation of flourishing on a diet of nails, penknives and match-boxes. The liver in Birds is remarkable for possessing two ducts, one opening as usual close to the pyloric end of the stomach and one into the distal end of the first loop of the intestine. The pancreas of Birds has from one to three ducts. It has been recently proved that the pancreas of all Amniota originates as three pouches of the intestine behind the pouches which give rise to the liver—a dorsal pouch and two ventral pouches. All these pouches divide

and give rise to tufts of tubes. The ventral ducts disappear, the tufts of tubes which were connected with them acquire secondary connections with the dorsal tuft whose duct now serves to discharge the products of all three tufts and which persists as the adult pancreatic duct. In Birds, however, all the three pancreatic ducts appear to persist. The intestine is folded into four or five loops,

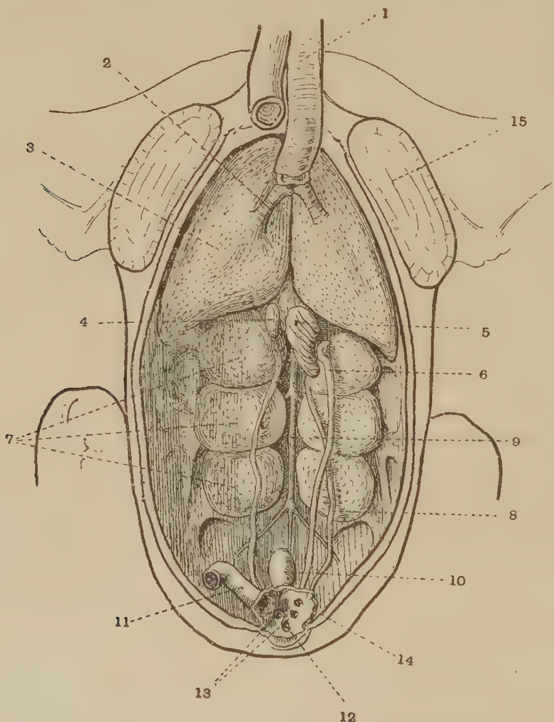

FIG. 313. The lungs, kidneys and gonads of a Pigeon, *Columba livia* $\times \frac{2}{3}$.

1. Trachea. 2. Bronchus. 3. Lung. 4. Suprarenal body. 5. Ovary. 6. Oviduct. 7. Lobes of kidney. 8. Ureter. 9. Aorta. 10. Bursa Fabricii. 11. Rectum. 12. Opening of bursa Fabricii. 13. Openings of ureters. 14. Opening of oviduct. 15. Cut pectoral muscle.

the arrangement of which has been made use of as a basis for classification. It ends by passing into a short rectum or large intestine, which is marked by a pair of out-growths, the intestinal caeca. Their size varies much, from long and wide blind sacs, as for instance in the Common Fowl, Ducks, Geese and other herbivorous birds, to quite small vestiges as in the Pigeon and in fish- and flesh-eating birds. The rectum ends in an enlargement termed the

urodaeum, the upper part of which receives ducts of the kidneys and reproductive organs, while into the dorsal wall of the lower and outer part a glandular pouch of unknown function, called the bursa Fabricii (12, Fig. 313), opens. This becomes smaller and sometimes entirely disappears in the adult Bird.

Urino-genital Organs.

The structure of the kidneys and reproductive organs is essentially the same as in the Reptilia. The metanephros in both sexes is distinctly divided into lobes. The mesonephros is represented by a small lobed epididymis closely adherent to the testes. The suprarenal body (4, Fig. 313) is homologous with the adrenal of Amphibia.

In most Birds there is no special organ for copulation, the whole end of the cloaca being turned inside out for this purpose, just as in Amphibia and Rhynchocephala. That this however is a secondary and not a primary state of affairs is suggested by the existence in Ostriches and some other Birds (Anseriformes) of a long penis on the dorsal wall of the cloaca similar in structure to one of the penes or copulatory sacs of the Lizard.

There is usually only one functional ovary, the left; an instance of the economy one observes throughout animated nature, for there is always a tendency when organs become expensive, that is, so large as to be a serious tax on the system, to reduce their number, and the production of eggs of the size of a Bird's is a great drain on the organism. In the case of a few birds of prey it has been recently shown that the right ovary can produce fully developed eggs as well as the left. There are two oviducts, but the right is small and useless. It must be remembered that the true egg formed by the ovary is the yolk; the white and the shell are additions derived from the oviduct.

Habits.

The nests which Birds build and their care for the nestlings, whom they in some cases feed at short intervals for about seventeen hours out of the twenty-four, are well known to all. Most also are aware that many birds migrate to other lands as winter sets in. It is less well known that quite as many migrate to lands further north on the approach of spring. Few imagine the enormous distances which are covered by birds on the wing. They constantly pass from the Bermuda Islands to the Bahamas, 600 miles, without a rest. Many species which have their home in North Africa go every spring to North Siberia to build their nests. They fly, when migrating, at such heights in the air as to be quite invisible and attain a pace which

seems hardly credible. There is no doubt, however, that very large numbers perish in crossing the sea.

Remains of fossil birds earlier than the tertiary period are very rare, but a few exceedingly interesting specimens have, however, been obtained. The principal of these is *Archaeopteryx*, represented by two specimens from the quarries in lithographic stone at Solenhofen in Germany. This remarkable bird had a long tail like that of a lizard, to each vertebra of which a pair of feathers was attached; the fingers of the wing bore claws and the bones of the palm (metacarpals) were free from one another. In the skull the premaxilla was as usual ensheathed in a horny beak but the maxilla bore teeth.

In all these points *Archaeopteryx* may be said to retain reptilian characters. Two other fossil birds (*Hesperornis* and *Ichthyornis*) had teeth in the maxillae but in other respects their structure was like that of modern birds.

Classification.

The classification of Birds presents great difficulties. They are a modern and very successful group of animals and evolution in them is proceeding rapidly. Older taxonomists were wont to classify them by the shapes of their beaks and their claws; modern taxonomists are perhaps too apt to reject these as external characters "of a purely adaptive nature." Such comments raise some fundamental questions on which a few words may be said here. If the evolution theory be justified all characters in animals are adaptive: they have either been directly acquired in response to the demands of the environment, or they are the secondary result of the adaptation of other organs to the environment. Now the thought underlying the distrust of external characters as a basis of classification is that they in their form represent the most recent adaptations since they come first into contact with the environment; the more deeply situated organs it is thought, are more slowly affected and hence represent more ancient adaptations, and therefore afford indications of the affinity of animals whose external features have become different. There is a good deal to be said for this principle but it must be used with caution. As Herbert Spencer pointed out long ago, the alimentary canal, the most internal organ of all, comes into close and direct relation to the environment.

The bones on which systematists are wont to lay what seems to us an overwhelming amount of stress alter quickly and directly according to the development of the muscles which are attached to

them and the development of these muscles is an expression of the habits of the animal—a feature which is eminently subject to adaptive variations.

Such organs as the heart, the kidneys and the genital organs are perhaps less variable than those we have just mentioned, but these afford little or no help in classifying birds since their structure throughout Aves is extraordinarily uniform. Another objection to using internal organs as a basis for classifying Aves is that the dissection of different types and the comparative description of the internal organs have been so incompletely accomplished that according to one of the best bird specialists, the external characters furnish just as reliable data as the ill-known internal organs. In classifying we must endeavour to group together birds showing as many points of agreement as possible and frankly admit that the question of the affinities of many groups is at present an unsolved problem. The points at present most relied on in classification are the structure of the palate and the amount of care given to the young. With regard to both these points we recognise in some birds archaic features which they share with the Reptiles. These enable us to separate a more primitive stratum from a more advanced stratum of Birds. Huxley long ago showed that four types of palate are found amongst modern birds which are as follows:

(1) The dromaeognathous palate. In this type the vomers are large and flat and embrace the rostrum of the basisphenoid bone behind and prevent the pterygoids and palatines from touching it. The pterygoids are united to the basisphenoid by processes termed basipterygoid processes. A palate such as this presents considerable resemblances to the palate of *Sphenodon*.

(2) The schizognathous palate. In this type the vomers coalesce in front to form a pointed bone; they are small behind and the pterygoids and palatines rest on the basisphenoidal rostrum and can play up and down on it. The maxillopalatine bones do not unite in the middle line.

(3) The aegithognathous palate. This type greatly resembles the preceding but differs from it in that the vomers unite in front to form a bluntly truncated bone and diverge behind.

(4) The desmognathous palate. In this type the vomers have the same form as in the second type but they are smaller and may occasionally be absent altogether. The maxillopalatine bones are united in the middle line so as to form a bony palate.

With regard to the care of the young, the Mound-builders of Australia (Megapodidae) exhibit the most primitive conditions, for they do not even sit on their eggs, but bury them in a mass of decaying vegetation, so that they may be hatched by the heat of fermentation just as Reptiles bury their eggs where they may be hatched by the heat of the sun. All other birds sit on their eggs. But in the case of some birds, such as the common hen, when the chicks are hatched they are covered with down and are able to run about and feed themselves: such chicks are said to be nidifugous. In the case of other Birds, such as the Swallow, the chicks emerge from the egg in a blind, naked condition and have to be fed with unremitting care by the parents: such chicks are said to be nidicolous: and this is certainly a more modified condition of affairs than the nidifugous condition.

If we now, starting from *Archaeopteryx*, ask ourselves what the most primitive form of bird was like, we may arrive at certain probable conclusions. Birds, we have already concluded are derived from Reptiles, and they must have originated from active tree-climbing Reptiles of moderate size, which jumped from branch to branch, for in this way only can we understand how the power of flying was evolved.

The wings in the first birds must have been actively functional, for only by their functional importance can we account for their evolution; but we need not credit the first birds with great powers of flight any more than the first aviators, whose short flights pale into insignificance in comparison with the flying feats of to-day. Now there is one group of birds which to a large extent retain these primitive characters to-day: these are the Game-Birds, the so-called Cock-like Birds (Galliformes). They roost in trees for the most part and make short flights only when they are disturbed or alarmed. Their young are nidifugous.

Included in this group are two remarkable genera. In one of these, the South American Tinamou, the palate is of the dromaeognathous type, and there is a penis in the dorsal wall of the cloaca. In the other (*Opisthocomus*) the chick, when it emerges from the egg, has claws on the thumb and index finger and the wing feathers are not developed, and for the first few days of its life it runs about over the branches like the arboreal reptile from which the group of Birds is descended. It is in fact a bird larva. In all other Galliformes, except the Tinamou, the palate is schizognathous and there is no penis. It is customary to separate the Tinamou on this account

from the other Game-Birds and make it the type of a primary division, the Tinamiformes, but in all essentials it is a Game-Bird which retains primitive characters. In one respect, however, the Game-Birds are not primitive, but secondary; they are for the most part grain eaters.

Now the primitive Birds had teeth, and we may assume that in its leaps from branch to branch the ancestral reptile chased something more active than seeds. With great probability we may conclude that the original bird was insectivorous, and it is useful to remember that this is true of the chicks of very many species the adults of which are not insectivorous.

A number of large flightless Birds agree with the Tinamou in possessing a dromaeognathous palate and in having a penis. These are grouped together as RATITAE, because the breast-bone has lost its keel and has become raft-like, and the clavicles have disappeared. These are secondary degenerative changes due to the loss of the power of flight, and another such change is found in the loss of barbules, in consequence of which the feathers have a soft downy consistence. This is because they are not required to form a firm surface with which to beat the air. It is this character which makes them prized for ornament.

The Ratitae include the true Ostrich (*Struthio*) from Africa with two toes, the Rhea from South America with three toes, the Emeu (*Dromaeus*) from Australia and the Cassowary (*Casuarius*) from New Guinea with three toes. All these species have powerful legs and can run at a great rate. Finally we have the Kiwi (*Apteryx*) from New Zealand with four toes, the smallest Ratite Bird, but in that country there formerly existed the largest of all Ratites, the Moas (*Dinornis*), which had thigh bones thicker than those of a horse. These, though now extinct, survived into the human period.

The Tinamiformes and Galliformes, and all other Birds, are grouped as CARINATAE, but this is a most illogical proceeding, as individual species among them have lost the power of flight, and lost in consequence, or very nearly lost, the carina or keel on the sternum. And the Ratitae are certainly not descended from a common Ratite ancestor, but represent different types of archaic birds which have independently lost the power of flight owing to the circumstances in which they have found themselves. In the Ratitae of New Zealand this was certainly due to the absence of carnivorous mammals.

Reverting now to Birds of more modern type and passing over the Galliformes, we find in the group of Divers (Colymbiformes)

aquatic, swimming and diving Birds with flattened legs nidifugous young and schizognathous palate. The Diver (*Colymbus*) is well known on our northern coasts; it is called the Loon in N. America. Another form common to England and N. America is the Grebe (*Podiceps*), in which the toes are fringed with separate webs not united into a common web. The Procellariiformes, which include the Petrel (*Procellarius*), and the Albatross (*Diomedea*), are also swimming and diving Birds, but they differ in being nidicolous and in retaining the curious primitive character in having the covering of the bill made up of several plates, recalling the scales of Reptiles, whereas in most Birds it consists of a single horny sheath, which no doubt has been produced by the fusion of several such scales. The Penguins (Sphenisciformes) are known to all frequenters of the London Zoological Gardens by the upright gait and curious paddle-like wings in which the feathers have degenerated into scales. The toes are webbed, for these also are swimming and diving Birds which use the wings as well as the feet to swim with. The palate is schizognathous. All the Penguins belong to the Southern Hemisphere.

More familiar are the Duck-like Birds (Anseriformes) distinguished by the series of transverse horny ridges on the palate, extending to the edges of the bill and enabling these Birds to either crop water plants or to hold struggling aquatic prey, like frogs. The toes are webbed and the palate desmognathous. The Anseriformes include all our Swans, Ducks and Geese.

Equally well characterised are the Birds of Prey or Falcon-like Birds (Falconiformes), distinguished by their powerful arched beak with cutting edges, the desmognathous palate and above all by the cruel curved talons on their toes. These claws are the real weapons of attack—the beak is only used to tear off the flesh of the prey when it has been killed. The Golden Eagle, our largest Bird of Prey, has been known to kill a full-sized cat with a single blow of its claws.

The Ciconiiformes, or Stork-like Birds, are a more diversified group. They have a desmognathous palate and usually a long spear-like beak, with which they impale the fish on which they feed. This group includes not only the Storks and Herons in which the legs are long and the toes free, but the so-called Steganopoda (Pelicans and Gannets), in which all four toes are included in one web and the legs are short.

The Gruiformes, or Crane-like birds, including the Cranes and Rails are often confounded with some of the Ciconiiformes, as many

of them are wading birds with long legs, but they are distinguished by having a schizognathous palate and by having the hallux or big toe inserted in the leg higher up than the other toes.

The Charadriiformes, or Plover-like Birds, include Plovers, Gulls and Pigeons. They are usually Birds with short legs and powerful wings. Like the Gruiformes, they have a schizognathous palate.

The Cuculiformes, or Cuckoo-like Birds, include the two very different groups of the Cuckoos and Parrots, united by the desmognathous palate and the turning of the fourth toe back parallel to the hallux; whether these two groups are really closely related is doubtful.

The Coraciiformes, Roller-like Birds named after the Roller (*Coracias*), include such diverse groups as Owls, Swifts, Kingfishers and Woodpeckers, and can only be described as a lumber room—a mere temporary convenience. Most of the Birds in it have weak legs and descend very little to the ground, and, though nidicolous, do not make nests, but live in holes.

The Passeriformes, or Sparrow-like Birds, distinguished by an aegithognathous palate and by being nidicolous and constructing nests, are to be regarded as the most finished products of bird-evolution. They include, besides Crows, Magpies, Shrikes, Swallows and Jays, all our native songsters, and in the sub-division Oscines alone, which includes the best songsters, there are 5000 species.

Sub-class I. ARCHAEORNITHES.

The three fingers and their metacarpals remain separate, each with a claw. Both jaws with alveolar teeth; tail without pygostyle; wings with well-developed remiges.

Only example, *Archaeopteryx*.

Sub-class II. NEORNITHES.

Metacarpals fused.

Division I. **Ratitae.**

Flightless; without a keel on the sternum; without a pygostyle. Coracoid and scapula fused.

Ex. *Struthio*, African Ostrich; *Rhea*, American Ostrich; *Dromaeus*, Emeu; *Casuarius*, Cassowary; *Apteryx*, Kiwi.

Division II. **Odontolcae.**

Marine, flightless, without sternal keel; teeth in furrows.

Ex. *Hesperornis* (extinct).

Division III. **Carinatae.**

Without teeth, with a keeled sternum.

Tribe 1. Colymbiformes (Divers and Grebes). Plantigrade, nidifugous, aquatic, toes webbed.

Ex. *Colymbus*, Diver; *Podiceps*, Grebe.

Tribe 2. Sphenisciformes (Penguins). Nidicolous; wings transformed into rowing paddles; feathers small and scale-like.

Ex. *Spheniscus*, Penguin.

Tribe 3. Procellariiformes (Petrels). Nidicolous, good fliers, pelagic; sheath of bill compound.

Ex. *Procellaria*, Petrel; *Puffinus*, Puffin; *Diomedea*, Albatross.

Tribe 4. Ciconiiformes. Nidicolous; swimmers or waders; desmognathous with basipterygoid processes.

Ex. *Sula*, Gannet; *Pelecanus*, Pelican; *Ardea*, Heron; *Ciconia*, Stork; *Phoenicopterus*, Flamingo.

Tribe 5. Anseriformes (Ducks and Geese). Nidifugous; desmognathous with basipterygoid processes; with copulatory organ; palate bearing hard, horny, parallel ridges.

Ex. *Anas*, Duck; *Anser*, Goose; *Cygnus*, Swan.

Tribe 6. Falconiformes (Birds of Prey). Nidicolous; desmognathous; beak powerful with decurved tip; talons long and curved.

Ex. *Falco*, Falcon; *Aquila*, Eagle; *Cathartes*, Turkey-Buzzard.

Tribe 7. Galliformes (Game-Birds). Nidifugous; schizognathous.

Ex. *Gallus*, Common Fowl; *Phasianus*, Pheasant; *Tetrao*, Grouse.

Tribe 8. Tinamiformes (Tinamous). Like Galliformes but without pygostyle and with dromaeognathous palate.

Ex. *Tinamus*, Tinamou.

Tribe 9. Gruiformes (Cranes and Rails). Waders, legs long, nidifugous; schizognathous.

Ex. *Rallus*, Rail; *Fulica*, Coot; *Grus*, Crane.

Tribe 10. Charadriiformes (Plovers, Gulls and Pigeons). Schizognathous, legs short.

Ex. *Charadrius*, Plover; *Larus*, Gull; *Pterocles*, Sand-grouse; *Columba*, Pigeon.

Tribe 11. Cuculiformes (Cuckoos and Parrots). Desmognathous, fourth toe either permanently reversed or reversible at will.

Ex. *Cuculus*, Cuckoo; *Psittacus*, Parrot.

Tribe 12. Coraciiformes. Nidicolous, but nest in holes, arboreal, legs feeble.

Ex. *Coracias*, Roller; *Upupa*, Hoopoe; *Alcedo*, Kingfisher; *Strix*, Barn-owl; *Caprimulgus*, Nightjar; *Cypselus*, Swift; *Picus*, Woodpecker.

Tribe 13. Passeriformes. Nidicolous, construct elaborate nests; aegithognathous.

Ex. *Passer*, Sparrow; *Turdus*, Thrush; *Hirundo*, Swallow; *Alauda*, Lark; *Corvus*, Crow.

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CHAPTER XXV

SUB-PHYLUM IV. CRANIATA

Division II. Gnathostomata

Sub-division II. Amniota

Class V. Mammalia

General Characteristics.

The class Mammalia (Lat. *mammae*, breasts), the last division of the phylum Vertebrata, includes those animals which suckle their young. Like the Birds, their temperature is constant and they have the ventricle of the heart completely divided into two halves. But they differ from Birds in never possessing feathers; only in one order is the fore-arm converted into a wing, and even in this case the arrangement of the parts is quite different from that in the Bird's wing.

Besides these characters however there are a large number of others in which, while Mammals differ from both Birds and Reptiles, the last-named two groups agree with one another, so that for a long time the opinion was held that Mammals were vastly further removed from Reptiles than were Birds; and indeed if only modern Reptiles were considered this could not well be denied. If however we examine the remains of the Reptiles which have existed on the earth in past time, we come to the conclusion that the better way to state the difference would be to say that, whereas Birds might be traced back to Reptiles not very unlike modern lizards, Mammals are derived from a type which has died out, leaving no modern representatives. Thus Mammals are almost certainly descended from the extinct group Theromorpha and birds from some Rhynchocephalan ancestor.

Just as feathers constitute an indubitable mark of a Bird, so true hairs are equally characteristic of Mammals. It is true that the word hair is loosely used, being often applied for instance to the delicate flexible spines of caterpillars, which are constructed on a totally different plan to the hairs of Mammals. A hair in the zoological sense is a rod composed of closely packed cells converted into horn, and under a microscope the outline of these cells can be

seen like a mosaic on the surface of the hair, the outermost ones overlapping each other like slates on a roof with the same function of letting the water run off.

We saw that a feather originated as a little knob, the outside of which was composed of horny cells, while the interior consisted of soft living tissue supplied with blood-vessels; a hair on the other hand makes its appearance as a cylinder of horny cells growing down from the epidermis into the dermis underneath. This cylinder then becomes split into an outer sheath and an inner core, the latter of which elongates and forms the hair, while the former remains

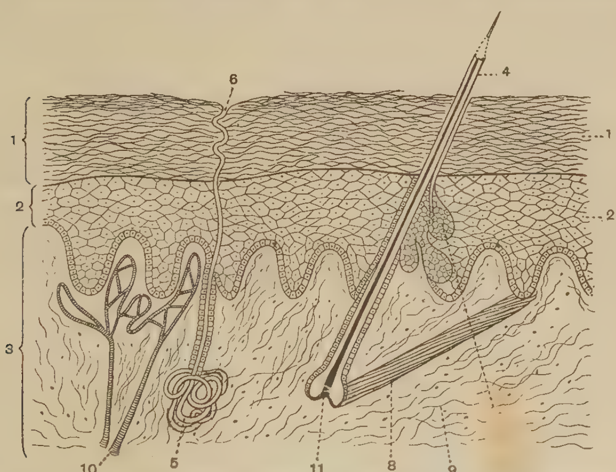

FIG. 314. Section through the skin of a Mammal. Highly magnified. Diagrammatic.

1. Outer layer of dead horny cells which are rubbed off from time to time, *Stratum corneum*. 2. Deeper layer of cells retaining their protoplasm, *Stratum Malpighii*. 1 and 2 form the epidermis and are ectodermal in origin. 3. Dermis or *Corium*. 4. A hair. 5. Sweat-gland. 6. Opening of the duct of the sweat-gland. 7. Sebaceous or fat gland. 8. Erector muscle of the hair. 9. Connective tissue fibres of the dermis. 10. Blood-vessel. 11. Vascular papilla at base of the hair follicle.

stationary and constitutes the follicle of the hair. The growth of the hair is rendered possible by a little plug of dermis carrying blood-vessels, which is pushed up into the lower end of the hair. In consequence of the rich supply of food brought by these vessels to the deep cells of the ectoderm lying above them, these cells bud off horny cells with great rapidity and persistence, and in this way a column of horny cells is formed which pushes out the older part of the hair and causes the whole structure to assume a great length, sometimes equalling that of the body. The plug of dermis

is called the papilla of the hair, it obviously corresponds to the knob of dermis in the base of the feather, and so a hair might be compared to a feather consisting only of the shaft and sunk in a very deep and narrow pit of the skin (Fig. 314). In a few cases hairs may be aggregated so as to form overlapping scales, and practically all Mammals have nails or claws on the fingers and toes which resemble essentially the horny reptilian scale.

There is one respect in which Mammals and Birds agree with each other and differ from all other kinds of animals, and this is that their body temperature is considerably higher than that of their usual surroundings and is capable of varying with safety to the extent of only a few degrees. This condition of a constant temperature is known as the homoiothermal (so-called "warm-blooded") condition and differs strikingly from the poikilothermal (so-called "cold-blooded") one of other animals, in which the body temperature varies with that of the surroundings and is usually only one or two degrees above the latter. The temperature of a Bird or Mammal is maintained constant by regulation both of the loss of heat by radiation at the surface and of the manufacture of heat by tissue oxidation.

Perspiration or sweat is also characteristic of Mammals. This consists of a fluid secreted by certain cells of the epidermis which remain soft and are not converted into horn like most of the outer cells. The cells which manufacture the perspiration are arranged to form long tubes called sweat-glands, which penetrate far below the epidermis into the dermis underneath (Fig. 314). The production of sweat is a factor in the regulation of the body temperature and by it also certain excreta leave the body. The fluid poured out carries off a certain amount of heat and by its evaporation cools the skin. Besides the sweat-glands there are other tubes which are invaginations of the epidermis and consist of a special kind of cell. These tubes, sebaceous glands, open into the hair follicles. They secrete the fatty substance or sebum which gives the natural gloss to the hair (Fig. 314).

Mammals, as we have seen, feed their young after they are born by suckling them, that is providing them with milk. This milk is a peculiar fluid produced by the mammary glands, consisting of epidermal tubes crowded together over certain areas of the ventral surface. They open at certain spots, raised above the general level, which constitute the nipple or teat. It has been recently shown that the mammary glands are simply enlarged and modified sebaceous

glands. In the lower Mammals these glands arise in connection with rudimentary hairs (the milk hairs) which are later shed.

As regards their internal structure the great differences between Mammals on the one hand and Reptiles and Birds on the other, are to be found in the skull, the brain and the limbs and, to a lesser extent, in the heart and the arrangement of the great arteries and veins.

Turning first to the skull, we find that in a Mammal instead of having only one knob or condyle to fit into a cup on the first vertebra, as is the case with Birds and Reptiles, the skull has two, which are projections of the exoccipital bones that wall in the sides of the foramen magnum, whereas in Birds the single condyle is an outgrowth of the basi-occipital bone that forms the floor of the foramen magnum (Fig. 315). In Reptiles, more especially the Chelonia, the so-called single condyle is really trifid, the lateral parts being

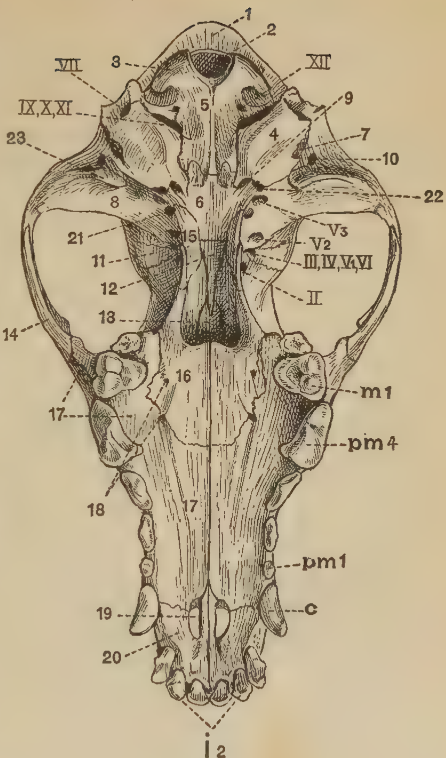

Fig. 315. Ventral view of the cranium of a Dog, *Canis familiaris* $\times \frac{3}{5}$.

1. Supra-occipital. 2. Foramen magnum. 3. Occipital condyle. 4. Tympanic bulla. 5. Basi-occipital. 6. Basisphenoid. 7. External auditory meatus. 8. Glenoid fossa. 9. Foramen lacerum medium, aperture through which the internal carotid passes to the brain. 10. Postglenoid foramen. 11. Alisphenoid. 12. Presphenoid. 13. Vomer. 14. Jugal. 15. Pterygoid. 16. Palatal process of palatine. 17. Palatal process of maxilla. 18. Posterior palatine foramen. 19. Anterior palatine foramen. 20. Palatal process of premaxilla. 21. Opening of tube in alisphenoid bone through which the carotid artery passes. 22. Hole for passage of Eustachian tube. 23. Process of squamosal to act as a stay for condyle of lower jaw.

II—XII. Exits of cranial nerves. i 2. Second incisors. c. Canine. pm 1, pm 4. First and fourth premolar. m 1. First molar.

formed by the exoccipitals and the basal one by the basi-occipital. From this condition it is easy to see how the conditions in Birds and higher Reptiles on the one hand and in Mammals on the other may have been derived. Then the brain instead of lying behind the eyes extends forward between and above them; there is consequently no interorbital septum, and the side walls of the brain-case are thoroughly and firmly ossified, not merely represented by a vertical plate imperfectly ossified, as in a Bird, or nearly entirely membranous, as in some Reptiles. These walls are in fact constituted behind by bones termed alisphenoids which in reality correspond to the epipterygoids of Reptiles (see p. 572). These "alisphenoids" are applied to the wall of the cranium above but below they diverge outwards and join the pterygoid bone just as do the epipterygoids in *Lacerta*. In front, the lateral walls of the cranium are constituted by orbitosphenoid bones, whilst a strong mesethmoid bone is developed in the internasal septum. This septum is prolonged beyond the bones of the face by a cartilaginous plate forming the support of a flexible nose or muzzle; this is a feature quite peculiar to Mammals. The base of the cranium is completely ossified, not only behind by the occipital and basisphenoid bones but in front by the presphenoid

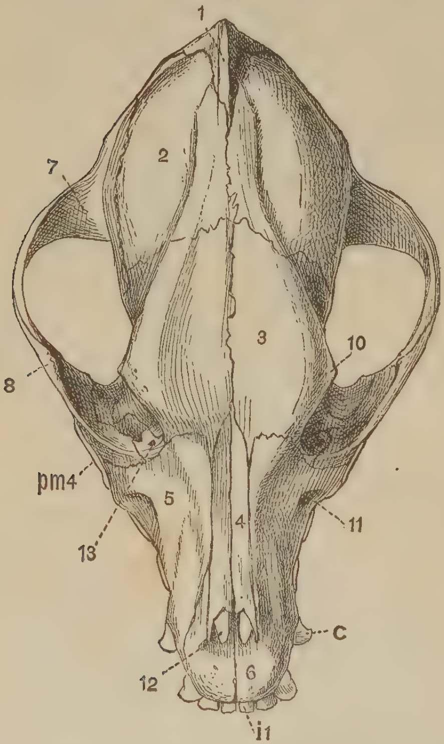

FIG. 316. Dorsal view of the cranium of a Dog, *Canis familiaris* × $\frac{2}{3}$.

1. Supra-occipital. 2. Parietal. 3. Frontal. 4. Nasal. 5. Maxilla (facial portion). 6. Premaxilla. 7. Squamosal. 8. Jugal 10. Postorbital process of frontal. 11. Infra-orbital foramen. 12. Anterior palatine foramen. 13. Lachrymal foramen. i 1. First incisor. c. Canine. pm 4. Fourth premolar.

bones. To the last-named a wedge shaped bone termed the vomer is attached which projects downwards and divides the air-space above the palatal folds into two. The name (Lat. *vomer*, ploughshare) is derived from the shape of the bone in Mammals; it is inappropriate as a description of its shape in other Craniata. Recent discoveries in the Theromorpha make it plain that the Mammalian vomer is the representative of the parasphenoid bone of Amphibia and the lower Reptiles. The vomers of Amphibia and Reptilia are represented in the Theromorpha by a pair of small bones termed prevomers attached to the underside of the internasal septum in front of the unpaired bone which corresponds to the vomer of Mammalia. The pterygoid bones take the form of thin vertical plates; they are attached throughout their whole length to the side wall of the cranium by the "alisphenoid." As in Crocodilia and desmognathous Birds the palatal folds are united in the middle line; the bones supporting them are processes of the premaxillary, maxillary and palatine bones. Between the pterygoid bones however the palatal folds form a purely muscular bridge, called the soft palate, which ends posteriorly in a projecting lobe, called the uvula, lying close to the glottis. The processes of the palatine bones always meet so as to form a bony bridge, called the hard palate; those of the premaxilla and maxilla do so to a certain extent, leaving however vacuities known as the anterior palatine foramina (19, Fig. 315). (The posterior palatine foramina are small holes in the palatine bones for the passage of blood-vessels.) As in Chelonia, there is only a lower temporal arcade, which is formed mainly by the cheek-bone or jugal. There is however no quadratojugal, and the jugal joins a process of the squamosal, which is a large bone covering the side of the skull and almost concealing the conjoined bones of the auditory capsule from view. It is characteristic of Mammalia that these bones, which in the embryo are distinct from one another, unite to form a single bone, called the peri-otic, which is fused to the squamosal. In Reptiles, on the other hand, the epi-otic joins the supra-occipital and the opisthotic the exoccipital, while the pro-otic remains distinct. The outer ear, the funnel-shaped passage leading into the tympanum, which is termed the meatus auditorius externus, is surrounded by a bone called the tympanic, often swollen into a rounded form and then termed the tympanic bulla. There is often a tube-like prolongation of this bone into the base of the ear-flap or pinna.

There is no quadrate recognisable as such, the lower jaw consisting of a single dentary bone on each side, which articulates with a smooth cup-shaped facet on the squamosal, called the glenoid cavity. Occupying the position of the prefrontal bone in Reptiles is a small bone called the lachrymal. This bone derives its name from the fact that it is pierced by a hole called the lachrymal foramen (13, Fig. 316) which permits of the passage of a duct leading from the orbit to the cavity of the nose. This duct carries

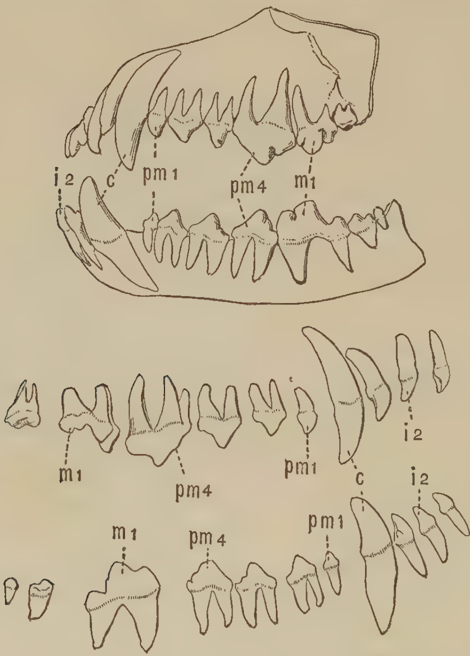

Fig. 317. Dentition of a Dog, *Canis familiaris* × ½.
i 2. Second incisor. *c*. Canine. pm 1, pm 4. First and fourth premolars. m 1. First molar.

off the excess of tears (Lat. *lacrima*, a tear), the secretion of the lachrymal gland, a development of the epidermis between the eyelid and the eye. The lip-bones, the premaxilla and maxilla, are well developed and like the dentary normally bear teeth, all of which are implanted in distinct sockets formed by the upgrowth of the bone which bears them. Many of these teeth are rooted, that is to say, after a certain time the dermal papilla on which the tooth is moulded becomes constricted at the base, so as to be

connected by only a narrow neck with the adjacent connective tissue, this appearing in the dried tooth as a small hole through which a blood-vessel passes. The term root is applied to the dentine surrounding the narrow neck. When it is formed, growth of the tooth ceases.

The teeth of Mammalia are amongst their most characteristic organs; they are more differentiated than those of other Craniata, and their peculiar structure enables us to identify many fossil remains as mammalian.

They are typically differentiated into four kinds, viz. incisors or cutting teeth, canines or stabbing teeth, premolars and molars, which taken together are termed cheek-teeth or back-teeth (Fig. 317). The incisors are borne by the premaxilla and have sharp, straight edges adapted for cutting morsels of convenient size from the food. The canines and hinder teeth are borne by the maxilla. The canines, popularly known as the eye-teeth, are pointed teeth used for the purpose of killing prey or for defence against enemies, or in the fights which occur among males for the possession of females. The premolars have at least one cutting edge, often two or more parallel to one another; they are used to cut up the morsels which have been taken into the mouth. Finally the molars have broad surfaces with which the food is sufficiently broken up to permit of its being swallowed. The teeth of the lower jaw are of course all borne by the dentary, and they are divided into the same varieties as those in the upper jaw. In Elasmobranchii, as we have seen, the teeth are enlarged placoid denticles developed on a fold of skin which is invaginated within the lip, and as one row of teeth becomes worn out another takes its place, the skin bearing the old teeth slipping forward over the lip. In the higher Craniata this fold is represented by a solid wedge of ectoderm, called the enamel organ, and in Amphibia and Reptilia it produces successive rows of teeth throughout life as they are needed. In Mammalia it normally produces two, the first of which lasts only for a short time during the youth of the animal, and is known as the milk dentition; the teeth belonging to this row are pushed out of the gum by those of the second row, or permanent dentition, which last throughout the life of the animal. In the milk dentition there are only incisors, canines, and molars; the milk molars are succeeded by the premolars of the permanent dentition, while the permanent molars have no predecessors and are regarded as belated members of the first dentition. The teeth of Mammalia have

undergone profound modifications in accordance with the different habits assumed by different members of the class, and are one of the principal features on which its division into orders is based.

From a study of the dentition of living Mammals the conclusion is arrived at that the typical number of teeth, that is to

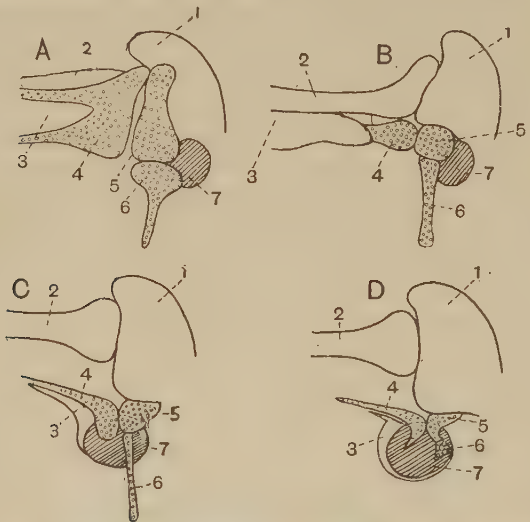

FIG. 318. Four diagrams to illustrate the evolution of the ear-bones in Mammalia. The diagrams represent the bones of the back of the lower jaw viewed from the inner side. The tympanic membrane is cross hatched and cartilage bones are covered with small circles, whilst membrane bones are left unshaded.

A. Condition in early Theromorphous Reptile. The articular and quadrate are large, and the dentary does not meet the squamosal.

B. Condition in later Theromorphous Reptile. The dentary has met the squamosal, and the quadrate and articular are reduced in size.

C. Condition in hypothetical form, the link between Theromorpha and Mammalia. The supra-angular has begun to extend along the border of the tympanic membrane.

D. Condition in primitive Mammalia (Prototheria).

1. Squamosal. 2. Dentary. 3. Supra-angular. 4. Articular (=Malleus). 5. Quadrate (=Incus). 6. Columella auris (=Stapes). 7. Tympanic membrane.

say, the number which the common ancestral form possessed, may be estimated at 44, i.e., 11 on each side of each jaw, made up of three incisors, one canine, four premolars, and three molars. This fact is expressed by the formula $\frac{3 . 1 . 4 . 3}{3 . 1 . 4 . 3}$, where the upper line denotes the teeth on each side of the upper jaw and the lower line those on each side of the lower jaw.

The apparent absence of the quadrate bone in the upper and of the articular in the lower jaw has given rise to much speculation as to what has become of these elements, which are so constantly present in Aves and Reptilia and are distinctly represented by cartilage even in Amphibia. For a long time the favourite theory was that they had been metamorphosed into the so-called ossicula auditûs or bones of hearing. In Anura, Reptilia, and Aves sound is conveyed from the ear-drum or tympanic membrane to the wall of the auditory capsule by a single rod, called the columella auris. In Mammalia however the connection is effected by a chain of three small bones called the malleus (Lat., hammer), incus (Lat., anvil) and stapes (Lat., stirrup) respectively, the last named being apposed to a membranous spot in the auditory capsule, called the fenestra ovalis, while the malleus is in contact with the ear-drum, and this theory has been practically proved to be true by the extensive series of discoveries of extinct Theromorphous Reptiles made in the last ten years. Some of these Reptiles have become so mammalian in their general appearance that their isolated teeth and bones would certainly be regarded as mammalian remains if they were found separated from the rest of the skeleton. In these Reptiles the dentary bone of the lower jaw becomes progressively larger and the other bones, including the articular, become smaller and crowded into the hinder angle of the lower jaw. This enlarged dentary acquires an articulation with the squamosal and the quadrate bone becomes reduced in size, till it is no larger than the columella auris with which it articulates. The stapes, since it rests against the fenestra in the peri-otic capsule, evidently represents the columella auris of Birds and Reptiles. The reduced quadrate represents the incus and the articular becomes the malleus. The tympanic bone, which encircles the outer ear and to which the ear-drum is attached, is not represented by cartilage, but is a dermal bone. It is believed to be the representative of the supra-angular bone which lies on the outside of the Reptilian lower jaw above the angular (Fig. 318).

This view of the homology of the ear-ossicle, which is deduced from the comparative anatomy of the Theromorpha is strongly supported by the developmental history of these ossicles in the higher Mammalia. The malleus is for a considerable time a block of cartilage, which is part of the rod forming the cartilaginous lower jaw and only becomes separated from it comparatively late in development, whereas the incus is segmented from the upper half

of the first visceral arch, as it should be if it represents the quadrate.

The chief peculiarity of the brain as compared with Reptiles is the greater development of the cerebral hemispheres, in

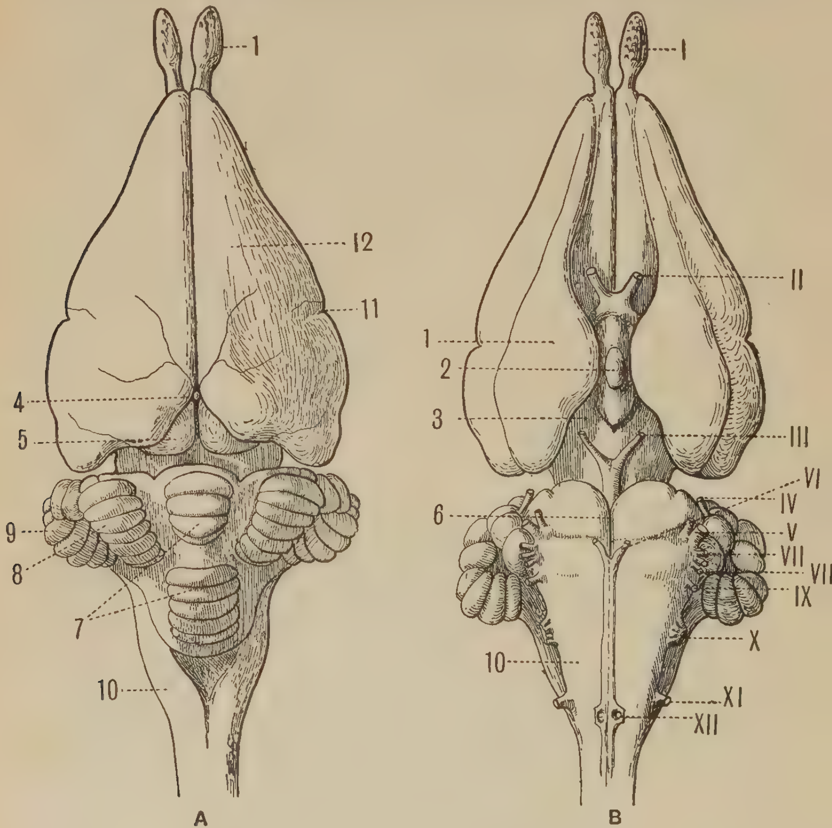

FIG. 319. Brain of Rabbit, *Lepus cuniculus* ×2.
A. Dorsal aspect. B. Ventral aspect.

1. Olfactory lobe. 2. Pituitary body. 3. Crura cerebri. 4. Pineal gland. 5. Anterior pair of corpora quadrigemina. 6. Pons Varolii. 7. Cerebellum. 8. Lateral lobe of cerebellum. 9. Floccular lobe of cerebellum. 10. Medulla oblongata. 11. Sylvian fissure separating the frontal lobe 12 from the temporal lobe behind. I. Origin of first or olfactory nerves. II. Optic or second nerves arising from the optic chiasma. III. Third or motor oculi nerve. IV. Fourth or patheticus nerve. V. Fifth or trigeminal nerve. VI. Sixth or abducens nerve. VII. Seventh or facial nerve. VIII. Eighth or auditory nerve. IX. Ninth or glossopharyngeal nerve. X. Tenth or vagus nerve. XI. Eleventh or spinal accessory nerve. XII. Twelfth or hypoglossal nerve.

proportion to the hind-brain or cerebellum. The former overlap completely and conceal the thalamencephalon and the mid-brain, and they are connected with one another by a great transverse band of nerve-fibres, called the corpus callosum. It is customary to map out the surface of the hemispheres into regions, in order to facilitate description in delimiting the areas concerned with the development of specific sensations and with the control of specific movements. These regions are called frontal, parietal, occipital, and temporal lobes. The temporal lobe is separated from the frontal by a deep groove, called the Sylvian fissure (11, Fig. 319, A). How well the increased size of the cerebrum is reflected in the shape of the cranium will be seen when it is recollected that the frontals and parietals, which represent merely the membrane covering the anterior fontanelle, not only form the roof of the cranium but a large part of its domed side wall; and further that the orbitosphenoid and alisphenoid, which are portions of the cartilaginous brain-case, are restricted to the base of the skull. The cerebrum has in fact protruded through the anterior fontanelle, pushing the membrane before it. The same condition is observable in Birds, but not in Reptiles or Amphibia. The cerebellum however is also well developed, just as in Birds, having indeed in addition to the lateral lobes an outer pair of lateral projections, called flocculi, embedded in a hollow of the bone that covers the inner ear (Fig. 319). The two halves of the cerebellum are connected with one another by a conspicuous band of fibres in the floor of the brain, called the pons Varolii.

The nose, except in aquatic Mammalia, is a highly developed sense-organ. The epithelium lining it is produced into scroll-like folds which are supported by thin plates of bone arising from the mesethmoid, and called ethmoturbinals. Above, where the mesethmoid joins the orbitosphenoid, so numerous are the apertures in it to allow the bundles of nerve-fibres from the olfactory cells to pass to the brain, that this part of the bone is reduced to a sieve, whence it has received the name of cribriform plate. From the maxilla, which forms the outer wall of the lower part of the nasal tube, a similar scroll-like bone, the maxilloturbinal, arises, which supports a corresponding fold of epithelium. This fold however is supplied only by the second division of the fifth nerve, and is not believed to have any olfactory function, but merely to act as a filter to free the inrushing air from grosser particles before it reaches the delicate olfactory epithelium.

The ear of Mammalia is distinguished by the development of a region termed the cochlea which is not present or at any rate clearly differentiated in the ears of the lower Vertebrates. It is a spirally coiled outgrowth of the sacculus of the ear, which replaces the simple retort-like lagena which is the outgrowth from the sacculus in Birds and Reptiles. From a study of its minute structure it appears that it is not the homologue of the lagena, which is still represented in Mammals by a slight vesicular enlargement of the tip

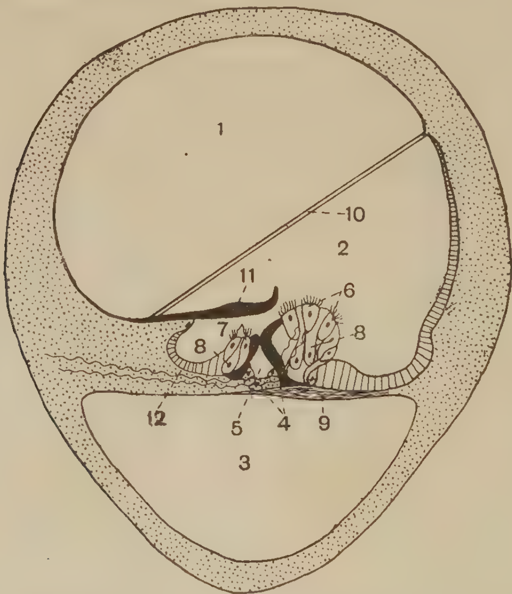

Fig. 320. Diagrammatic transverse section of the bony cochlea and its contained sense-organ in a Mammal.

1. Scala vestibuli. 2. Scala media (the real sense-organ). 3. Scala tympani. 4. The pillars of Corti. 5. The tunnel of Corti. 6. Outer auditory cells. 7. Inner auditory cells. 8. Supporting cells. 9. Basilar membrane. 10. Reissner's membrane. 11. Membrana tectoria. 12. Auditory nerve.

of the cochlea, but is rather a special development of the region at the base of the lagena connecting it with the sacculus. The special peculiarity of the cochlea is the organ of Corti, a development of the epithelium forming the basal wall of the cochlea. This consists of a double series of articular rods meeting each other above like the beams of a roof. Between the opposite members of the series is a space, the so-called tunnel of Corti. On the outer side of each series are several rows of sensory (auditory) cells each carrying

numerous short hairs. Underlying the sensory epithelium between the divergent legs of the rods of Corti and beyond them is stretched a connective tissue membrane consisting of parallel fibres termed the basilar membrane, and one theory of hearing is that these fibres vibrate like piano strings in harmony with tones of different pitch and stimulate the hair cells above them. The roof of the cochlea is a thin layer of cells termed Reissner's membrane (10, Fig. 320), and from the inner side of the cochlea a flap termed the membrana tectoria projects into its cavity. This is supposed to act as damper to the vibrations of the sense-hairs when these vibrations become excessive. The cochlea, often termed the membranous cochlea or scala media, is enclosed in an expansion of the peri-otic capsule of the same shape termed the osseous cochlea. Inside the osseous cochlea run two lymph spaces, one lying above the membranous cochlea, termed the scala vestibuli, and the other below the membranous cochlea, termed the scala tympani. These two spaces communicate with one another round the tip of the membranous cochlea. The scala tympani ends externally against a membranous window in the peri-otic bone termed the fenestra ovalis. There is another membranous window in the same bone called the fenestra rotunda, behind which lies the scala vestibuli and against which the stapes impinges externally, and when a vibration strikes the ear-drum, it is transmitted by malleus, incus and stapes to the fenestra rotunda and hence when it reaches the top of the cochlea to the scala tympani. Along the lymph in this it comes till it reaches the base of the cochlea. As the pulse passes along the scala tympani it is transmitted through Reissner's membrane to the cavity of the sense organ or scala media. Thus it stimulates the hair cells which respond to tones of different pitch and hence

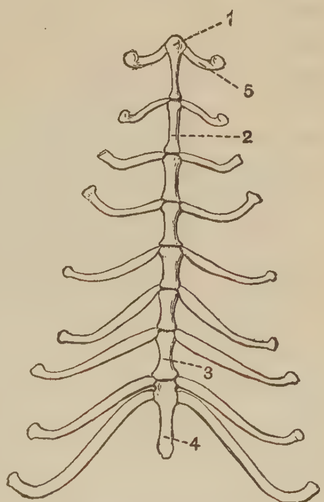

FIG. 321. Sternum and sternal ribs of a Dog, *Canis familiaris* × ½.

1. Presternum. 2. First sternebra of mesosternum. 3. Last sternebra of mesosternum. 4. Xiphisternum. The flattened cartilaginous plate terminating the xiphisternum is not shown. 5. First sternal rib.

apparently only the Mammal has an apparatus for analysing a sound-disturbance into its component parts. The outer ear or ectodermal involution leading to the drum is in Mammalia guarded by an external lobe termed the pinna of the ear.

The neck region of Mammals (with rare exceptions) always consists of seven vertebrae, and thus whereas a long-necked Bird like a Swan has numerous short vertebrae in this region, in a long-necked Mammal like the Giraffe the same region consists of seven immensely long vertebrae. The sternum of Mammals also is peculiar, consisting of distinct pieces or sternebrae. The first of these is called the presternum, and bears a crest for the attachment of the pectoral muscles; the last ends in a spade-like xiphoid cartilage, and is called the xiphisternum. The intervening segments constitute the sternebrae of the mesosternum. The lower ends of a pair of ribs are attached opposite the junction of two sternebrae (Fig. 321). The division of the sternum into segments is supposed to be due to the strains exercised on it by the sternal ribs owing to their movements in aid of respiration.

In Mammalia as in other Amniota the centrum is formed from the ventral intercalaries, and the head of the rib is articulated between two vertebrae; the articulation is not shifted on to the vertebra as in Crocodilia. The vertebrae have occasionally in the neck region cup and ball articulations like those of Amphibia, Reptilia and Aves, but elsewhere the thick intervertebral cartilage allows of sufficient bending, and the centra have flat ends which ossify late and for some time form separable discs of bone called epiphyses. These do not represent any new elements in the centrum, but only a method of ossification found in the limb-bones of Amphibia, Reptilia and Aves as well as in Mammalia. This method is as follows: the ensheathing membrane or periosteum first forms a tube of bone round the centre of the cartilage, the ends of which remain soft and capable of further growth; these terminal "epiphysial" cartilages are only replaced by bone when growth is diminishing, and are united with the main ossification when growth has ceased.

In the fore-limbs of Mammals the chief point to be noticed is the reduction in size of the pectoral girdle to which the fore-limbs are attached. The lower part of this, the coracoid, which in Birds and Reptiles is a large, strong bone meeting the sternum, is here, with the exception of a few primitive forms, a small hook with no connection at all with the sternum. Hence the pectoral girdle is much more movable than is elsewhere the case, and takes

part in the movements of the limb. It is therefore not surprising to find that the upper portion of the girdle, the shoulder-blade or scapula, is broad, affording a large surface for the attachment of

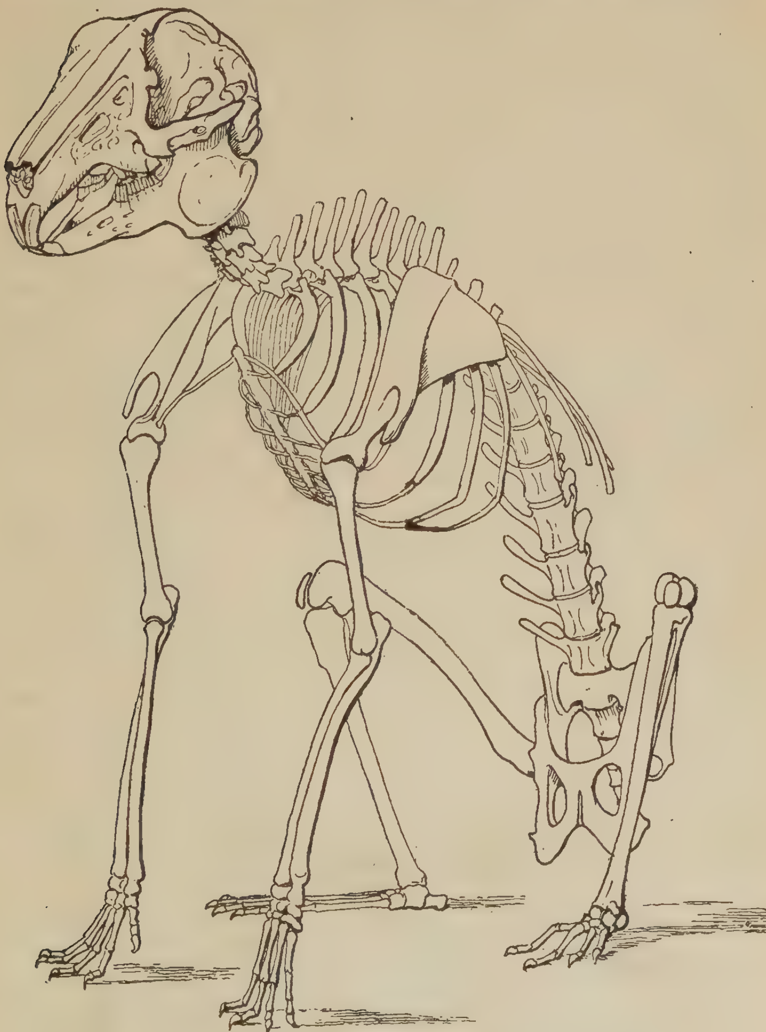

FIG. 322. Skeleton of Rabbit, *Lepus cuniculus* × $\frac{2}{3}$. In sitting position.

muscles; and that its surface is still further increased by the presence of a sharp vertical ridge rising up along its middle line (Fig. 322). To the end of this spine, as it is called, the

collar-bone or clavicle is attached; this bone extends inwards to the sternum and is loosely connected with it. In some Mammals the clavicle is absent.

The general form of the pelvic girdle to which the hinder limbs are attached is not very unlike that of Birds; but there are two important differences. First, the ilia or hip-bones are attached only for a very short distance to the backbone; and secondly, the lower bones of the girdle, the pubis and ischium, meet their fellows of the opposite side in front of the belly beneath the anus, whereas in Birds they do not even approach each other in this place, though in *Rhea* the ischia do meet dorsal to the anus.

The leg of Mammals differs from that of Birds and Reptiles in that the ankle-joint is situated between the bones of the shank (the tibia and the fibula) and the small bones of the ankle, instead of in the middle of these small bones (Fig. 322). The heel-bone or calcaneum is one of the uppermost tier of ankle-bones and corresponds to the bone called fibulare in the general scheme of the pentadactyle limb. It is prolonged into the heel, to which the great gastrocnemius muscle which forms the calf of the leg and which raises the heel is attached.

Turning now to the blood system of Mammals we find that the red blood corpuscles which give the colour to the blood are unlike those of other Vertebrates. They have no nuclei and are biconcave, while they are also much smaller and (except in Camels and Llamas) are circular, not oval discs as in all lower Vertebrates. Like Birds, but unlike most Reptiles, the Mammals have a four-chambered heart; the main blood-vessel, the aorta, is supplied by the left systemic arch alone, the right one being cut off from connection with it and being represented by the common trunk of the right carotid and subclavian arteries, the so-called innominate artery (Fig. 323), this being exactly the converse of the arrangement in Birds.

The ventral carotid arteries, which we have seen are reduced in Birds as compared with Reptiles and Amphibians, are usually absent in Mammals, though they may exist as quite small vessels—but the trachea and other structures in the neck receive blood from the common or dorsal carotid on its way to the head. The subclavian artery is of the dorsal type as in Lizards and Amphibians in all Mammals except Cetaceans, in which order the fore-limb or paddle obtains blood by an artery corresponding in origin with that to the fore-limb of Chelonians, Crocodiles and Birds, i.e., a

"ventral subclavian." The "dorsal subclavian" possessed by most Mammals is also found in Cetaceans, but it is distributed to the ribs and their muscles as the "intercostal artery."

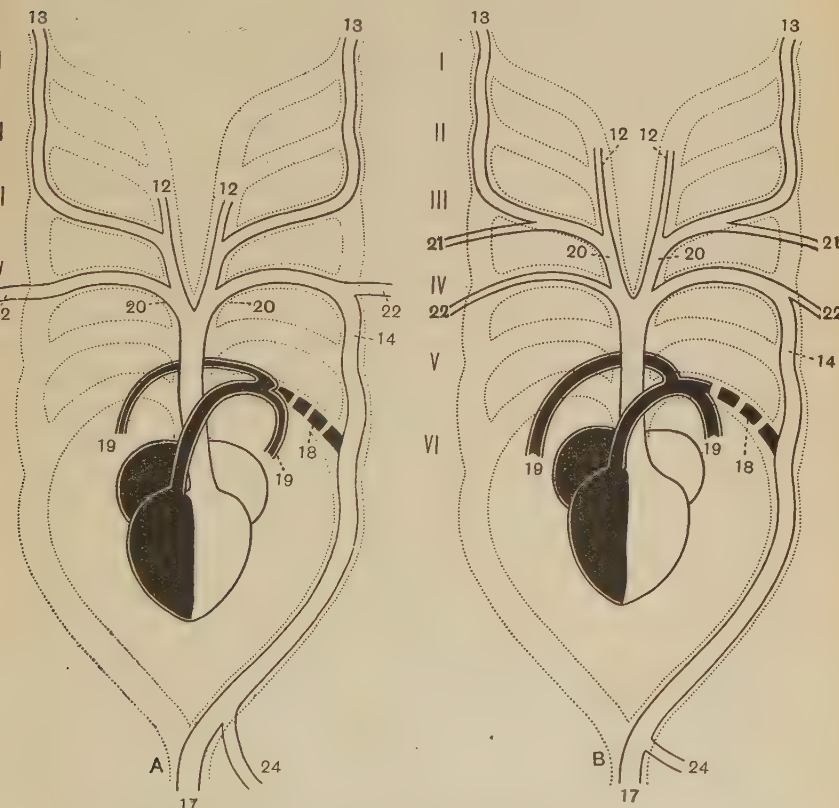

Fig. 323. Diagram of arterial arches of Mammals, viewed from the ventral aspect.

A. Of all Mammals except Cetaceans.

I, II, III, IV, V, VI. First to sixth arterial arches. 12. Ventral carotid (small or absent). 13. Common carotid (dorsal carotid). 14. Systemic arch. 17. Dorsal aorta. 18. Ductus arteriosus which in the embryo connects the pulmonary and systemic arteries. 19. Pulmonary. 20. Innominate. 22. Subclavian (dorsal type). 24. Coeliac.

B. Of Narwhal, representing Cetaceans.

I, II, III, IV, V, VI. First to sixth arterial arches. 12. Ventral carotid (small). 13. Common carotid (dorsal carotid). 14. Systemic arch. 17. Dorsal aorta. 18. Ductus arteriosus. 19. Pulmonary. 20. Innominate. 21. Subclavian (ventral type). 22. Intercostal (equivalent to subclavian of dorsal type). 24. Coeliac.

It is an interesting feature of the arterial system of a Mammal that in consequence of the embryo receiving its oxygen from the maternal blood, the connection between the systemic and pulmonary arches persists in an unreduced condition until birth. This connection is known as the ductus arteriosus, and through it the blood from the right ventricle is passed direct to the dorsal aorta. The pulmonary arteries are quite small during this period, and by these arrangements circulation of blood through the as yet functionless lungs is avoided. At birth the ductus arteriosus shrinks and is rapidly reduced to a solid cord, while the enlarging pulmonary vessels provide for the deviation of the venous blood to the now expanded lungs (18, Fig. 323).

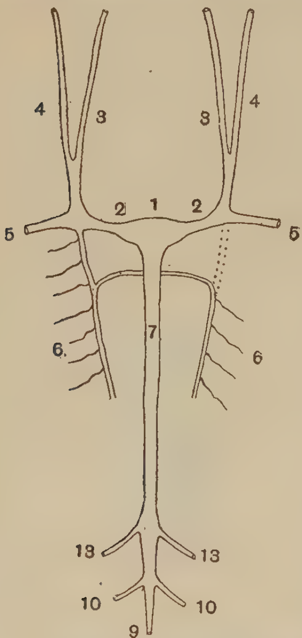

Fig. 324. Diagram to show arrangement of the principal veins in a Mammal.

1. Sinus venosus—gradually disappearing in the higher forms. 2. Ductus Cuvieri = superior vena cava. 3. Internal jugular = anterior cardinal sinus. 4. External jugular = sub-branchial. 5. Subclavian. 6. Posterior cardinal front part = venae azygos and hemiazygos. 7. Inferior vena cava. 9. Caudal. 10. Sciatic = internal iliac. 13. Femoral = external iliac.

In the venous system the blood from the head is returned by external and internal jugular veins, the former being much the larger. The caudal vein is continued directly into the inferior vena cava, so that there is no longer even the outward appearance of a renal portal system. This is due to the formation of a cross connection or anastomosis between the two posterior cardinal veins immediately behind the kidneys and to the subsequent disappearance of the right posterior cardinal in front of this, the left posterior cardinal extending through the subcardinal branch round the inner side of the left kidney to join the inferior vena cava where it issues from the kidneys. In consequence of this re-arrangement the left posterior cardinal assumes the appearance and functions of a posterior portion of the inferior vena cava. The right posterior cardinal persists only as the right common iliac vein into which the veins of the right leg empty themselves and as the

right renal vein. The anterior portions of the posterior cardinals, however, persist as the venae azygos and hemiazygos, which on each side receive the veins from the spaces between the ribs—the intercostal veins. Only that on the right—the vena azygos—reaches the ductus Cuvieri (superior vena cava); the left cardinal or vena hemiazygos develops a transverse branch through which its blood joins that of the right cardinal (Fig. 324).

One of the most interesting peculiarities of Mammals is their breathing mechanism. It will be remembered that whereas the Amphibia simply swallow air, in the Reptiles the size of the chest cavity is enlarged by pulling the ribs forward and then separating them, and as the lungs are closely attached to the wall of the chest, they are likewise enlarged and air rushes into them. In Mammals this same mechanism exists, but in addition there is a totally independent means of pumping air into the lung. This is rendered possible by the existence of a diaphragm, a partition convex in front which separates the coelom of the chest from the rest of the body-cavity. This partition is partly muscular, and when the muscle contracts the whole membrane is tightened and necessarily flattens, with the result that the chest-cavity is enlarged and air enters the lungs. The action of the diaphragm in fact is precisely similar to that of the muscular floor of the mantle-cavity of the Snail (see p. 287). The diaphragm is attached ventrally to the xiphoid cartilage, dorsally to the vertebral column, and laterally to the ventral edges of the hinder ribs which do not reach the sternum. By it the coelom of the Mammal is separated into a thoracic division in front and an abdominal one behind. The thoracic division is divided into two pleural cavities, one surrounding each lung, by the pericardium. Since all the vertebrae which bear recognisable ribs which reach the sternum belong to the thoracic region, they are termed thoracic vertebrae, while the ribless vertebrae of the abdominal region are denominated lumbar.

In the digestive system the principal peculiarity of Mammals is the high state of development of the salivary glands. These glands are much branched tubular outgrowths of the ectoderm of the mouth-cavity or stomodaeum; they secrete a fluid which moistens the food and is swallowed with it, thus helping digestion. They are foreshadowed by small glands in Frogs and Snakes, but in Mammals they form four large masses, viz. the sublingual, underneath the tongue, the submaxillary, under the angle of the jaw, the parotid, just under the ear, and the suborbital inside

the orbit. The ducts of all four open into the buccal cavity. Glands in similar positions are found in some Birds, but those of Mammalia secrete in addition to mucus a ferment, called ptyalin, which turns starch into sugar, so that the secretion which is called saliva is a true digestive juice. The large development of the large intestine causes most of the water to be absorbed from the undigested residue of the food, thus reducing it to a semi-solid mass or faeces, which is also a characteristic of the Mammalian alimentary canal.

Classification.

Mammals are divided into three great primary divisions or sub-classes according to the structure of the ovary and oviduct and to the stage of development attained by the young at birth. The lowest forms have comparatively large eggs like those of birds in which abundance of yolk is developed: in the higher forms the egg is at first small but has the power of absorbing nourishment from the wall of the oviduct, which is here enlarged to form a womb or uterus. In the highest division a special organ for the nourishment of the embryo, the placenta, is developed, as an enlargement of the embryonic bladder.

The sub-classes are called:

I. Prototheria, or primitive Mammals.
II. Metatheria, or modified Mammals.
III. Eutheria, or perfect Mammals.

Sub-class I. Prototheria

The Prototheria include two extraordinary animals, the *Ornithorhynchus* (*Platypus*), or Duck-billed Mole, and the *Echidna*, or Spiny Ant-eater, which are found only in Australia, New Guinea and Tasmania. In these animals large eggs with a firm shell are laid in a nest and incubated by the mother, and in harmony with this arrangement the two oviducts are large throughout the whole of their length, and do not join each other at any point but open along with the intestine into a common vent or cloaca, as is the case with Birds and Reptiles. The ureters do not open into the bladder as they do in all other Mammalia, but they and the bladder open separately into the cloaca. In the male a copulatory organ or penis is present lying beneath the ventral wall of the cloaca and opening into it in front and protruded from the cloaca behind. After they are hatched the young receive milk from the mother.

There is no teat, but the fluid from the milk-glands seems to soak into the hair and thence is sucked by the young. Before birth

Fig. 325. The Duckbill, *Ornithorhynchus anatinus.*

the young receive a certain amount of nourishment from the mother but the egg does not become adherent to the wall of the oviduct. The egg of *Echidna* for instance swells from a diameter of 2 millimetres to a diameter of 4 millimetres and more in its passage through the oviduct. A considerable amount of food is supplied by the abundant yolk in the egg. After birth the egg is carried by the female *Echidna* in a ventral pouch of skin on the abdomen. The female *Ornithorhynchus* has no such pouch.

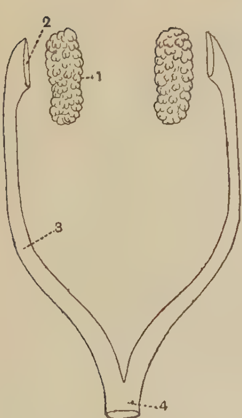

Fig. 326. Diagram to illustrate the arrangement of the female genital ducts in the Prototheria.

1. Ovary. 2. Oviducal funnel. 3. Oviduct. 4. Opening into cloaca.

The skeleton of the Prototheria presents many interesting features of agreement with the Reptiles; thus the vertebrae have no epiphyses, and there is not only a complete coracoid articulating with the sternum, but also two precoracoids which

overlap. Underneath these there are two clavicles and a T-shaped interclavicle, so that the shoulder-girdle recalls the complicated one of the Lizard.

Ornithorhynchus has webbed feet and lives in the water, feeding on worms and insects, which it digs out of the mud by its broad, shovel-like snout, whence the name Duck-bill (Fig. 325). It crushes its prey by means of horny plates, which are really patches of the hardened gum: when it is young, however, it has true calcareous teeth, two or three on each side of each jaw, but these it loses when it grows older. These teeth are covered by several rows of small points or tubercles. Similar teeth are found amongst the oldest remains of Mammals which are known, the so-called Multituberculata.

Echidna lives on ants and other insects, which it ensnares by putting out its tongue covered with sticky saliva. Like other ant-eaters it has a long snout and no teeth. It is covered with stiff spines like a porcupine.

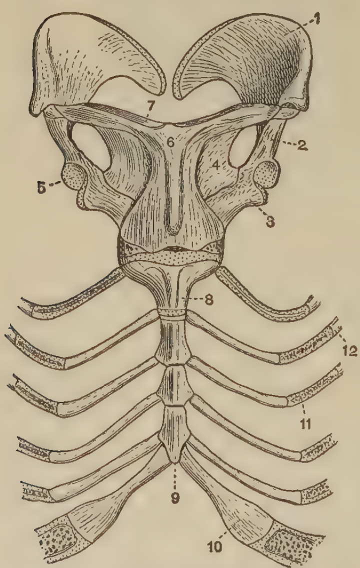

Fig. 327. Ventral view of the shoulder-girdle and sternum of a Duckbill, *Ornithorhynchus paradoxus* × $\frac{3}{4}$. After Parker.

1 and 2. Scapula. 3. Coracoid. 4. Precoracoid. 5. Glenoid cavity. 6. Interclavicle. 7. Clavicle. 8. Presternum. 9. Third segment of mesosternum. 10. Sternal rib. 11. Intermediate rib. 12. Vertebral rib.

Sub-class II. Metatheria.

The division Metatheria includes the curious pouched Mammals of Australia and the neighbouring islands and the Opossums of America. In these animals the egg is exceedingly small, and the egg-tube is divided into an upper part of correspondingly narrow diameter, called the Fallopian tube, and a lower, wider part, called the uterus. In this latter the small egg lies for a while. The egg-shell disappears and the egg then develops a close adhesion with the wall of the uterus. Through this adhesion nourishment is absorbed and the embryo in consequence grows and develops

rapidly. The allantois, however, always remains small and though in one or two cases it may contract an adhesion with the outermost layer of cells of the developing egg and through this with the wall of the womb yet this adhesion is temporary and does not persist till birth. Most of the nourishment is absorbed through an adhesion between egg and womb in the ventral region of the yolk-sac. Beneath the uterus comes the lowest part of the egg-tube, the so-called vagina. The two vaginae come into close contact with each other above and then diverge, both opening below apparently into the lowest part of the bladder, as do the vasa deferentia in the male. What seems to be the lowest part of the bladder is really the front portion of the cloaca, which has become separated from the part behind that receives the opening of the intestine. This common vestibule for excretory and reproductive ducts is called the urino-genital sinus, and its opening is distinct from that of the intestine or anus, although the two openings are still surrounded by a common muscle. From the spot where the vaginae meet above a pouch called the median vagina is often developed. This ends blindly in the young female, but in the mature female it acquires an opening into the urino-genital sinus and through this opening the embryo is born, the lateral vaginae serving merely to admit the spermatozoa from the male.

The penis or copulatory organ is a thickening surrounding the opening of the urino-genital sinus in the male, it is directly continuous with the neck of the bladder, and through it with the vasa deferentia.

When the young are born they appear not as eggs but as little mammals, which are however exceedingly small in size. They are then placed by the mother, who is said to transfer them with her lips, in a pouch made by a fold of skin on the lower part of her body, whence the name Marsupials (Lat. *marsupium*, a pouch), often given to these animals. A pair of sesamoid or epipubic bones run forward from the pubes. They are ossifications of a tendon of the external oblique muscle. Similar structures are found in

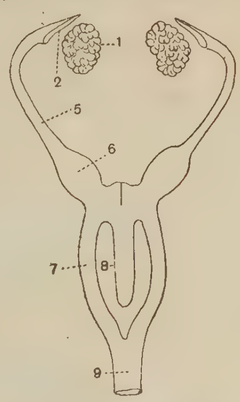

FIG. 328. Diagram to illustrate the arrangement in the female genital ducts of the Metatheria.

1. Ovary. 2. Oviducal funnel. 5. Fallopian tube. 6. Uterus. 7. Vagina. 8. Median vaginal pouch. 9. Urino-genital vestibule.

Prototheria, in Crocodiles and in Urodela. The young are quite incapable of feeding themselves, but each becomes attached to the opening of one of the ducts of the milk-gland, and the area of attachment becomes drawn out into a teat, and therefore the

FIG. 329. *Petrogale xanthopus.* The Rock Wallaby with young in pouch. After Vogt and Specht.

mother by compressing the muscles of the belly squeezes the milk-gland and forces milk down their throats. In order to allow the young one to breathe at the same time, the back of the soft palate is wrapped round the upper end of the windpipe, which

projects into the throat so that the air passes from the nose straight down the windpipe whilst milk flows down at the sides of the air-passage into the stomach. The pouch is however absent in some of the more primitive Marsupials, and recent research has demonstrated that it has arisen by the fusion of a number of separate depressions, one of which is formed round the attachment of each embryo.

In the mandible the angle, that is to say the lower and posterior end, is as a rule prolonged inwards as a horizontal shelf of bone. By this feature fossil skulls are recognised as belonging to the Metatheria.

The living Metatheria are divided into two great orders, of which the first is mainly carnivorous and the second herbivorous, though some members of both are insectivorous. The first order is termed

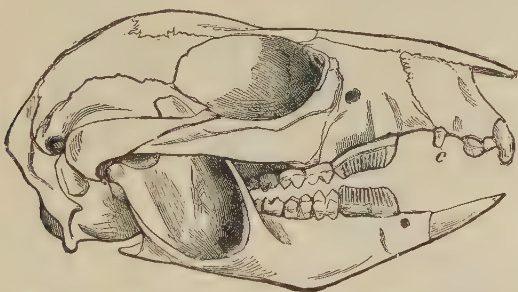

FIG. 330. Skull of Lesueur's Kangaroo-rat, *Bettongia lesueuri*. To exhibit Diprotodont type of dentition.

POLYPROTODONTIA; the animals composing it have at least four incisors on each side of the upper jaw and three on each side of the lower, whence the name (Gr. πολύς, many; πρῶτος, foremost; ὀδούς, ὀδόντες, teeth). The DIPROTODONTIA, as the second order is called, derive their name from the circumstance that in the lower jaw there is one large pointed incisor on each side, the others being rudimentary or absent, so that only two prominent teeth are observable (Gr. δίς, doubly). The Polyprotodontia are represented in America by the family of the Opossums, DIDELPHYIDAE, which is confined to that continent. It includes 24 species, most of which are found in Mexico, Central America, and Brazil, but one, the Virginian Opossum, *Didelphys virginiana*, ranges north as far as the south bank of the Hudson river. In all the Didelphyidae the great toe is large and can be separated from the other toes so as with them to grasp a support; thus it is said to be "prehensile." In

many of the more primitive Didelphyidae there is no pouch. In Australia the Polyprotodontia are represented by three families, viz. the Dasyuridae, the Peramelidae and the Notoryctidae. The first family includes the animals known as native Cats, which resemble the American Opossums, but are distinguished from them by the smaller number of incisor teeth and by having a rudimentary first digit in both fore- and hind-feet, whereas in the Didelphyidae, as we have seen, this digit is long and prehensile. The largest member of the family is *Thylacinus cynocephalus*,

Fig. 331. Banded Ant-eater, *Myrmecobius fasciatus* × $\frac{1}{2}$.

the Tasmanian Wolf, now confined to the wilder parts of Tasmania: it has a skull which strikingly resembles that of a Dog; in its habits it resembles a Wolf and is very destructive to Sheep. The Banded Ant-eater, *Myrmecobius fasciatus*, is an aberrant member of the same family which lives on insects, capturing them with its long tongue. The insects are made to adhere to this organ by the viscid saliva. The teeth, though rudimentary, are distinct. There is no pouch: the young when first born cling to the teats and conceal themselves in the long hair of the mother's abdomen. The Peramelidae or Bandicoots are small animals

somewhat resembling Rabbits and Hares in their appearance but with pointed muzzles; they are remarkable in possessing a type of foot characteristic of the Diprotodontia. The NOTORYCTIDAE include the single genus *Notoryctes*, which in habits and appearance resembles the Mole, a similar mode of life having brought about similar modifications of structure.

The order DIPROTODONTIA includes a number of species confined, with one exception, to Australia and the neighbouring islands. One species, the only living representative of the family EPANORTHIDAE, has been recently found in South America. This animal, which has received the name *Caenolestes uliginosus*, has feet like the DIDELPHYIDAE, and this circumstance renders it possible that it has been independently evolved from that family, whereas the other members of the order seem to have been derived from forms like the PERAMELIDAE. The typical Diprotodontia have the second, third, fourth and fifth toes of the hind-foot united by a web of skin. The fourth is the strongest toe, the fifth is a little shorter, but usually nearly as stout as the fourth; the second and third, though as long as the fourth, are much more slender, while the great toe is often rudimentary. Exclusive of the EPANORTHIDAE there are three families in the sub-order. The first family, the PHASCOLOMYIDAE, consists of one genus, *Phascolomys*, the Wombat, represented by three species. The PHASCOLOMYIDAE are distinguished by possessing only one incisor on each side of the upper jaw, and as both upper and lower incisors are chisel-shaped the dentition resembles that of a Beaver or Rat. Wombats are heavy animals with a shuffling gait, about the size and appearance of a Badger.

The second family, the PHALANGERIDAE, or Australian Opossums, have normally three incisors on each side of the upper jaw; the fore- and hind-limbs are of about the same size and the great toe is prehensile. These are small animals which like Squirrels live in trees, and several species possess a parachute-like membrane extending from fore- to hind-limb, by the aid of which they sustain themselves in the air during their great leaps from tree to tree. *Phascolarctus*, the so-called Native Bear, is a clumsy tailless Phalanger, in which the prehensile great toe is specially well developed. The MACROPODIDAE, or Kangaroos, are the most peculiar family of Diprotodontia, and indeed of the Metatheria. They resemble the Phalangeridae in having three upper incisors on each side, but differ totally in the structure of the limbs. The fore-limbs are so small

as to be used only for grasping, and locomotion is effected by a series of leaps carried out by the hind-limbs aided by the powerful tail. The sole of the hind-foot is excessively narrow, the second and third digits being represented by bones so slender that they take no part in supporting the body. *Macropus giganteus*, the Gray Kangaroo or "Old Man," may attain a height of from 4 to 5 feet. The fourth toe of the hind-foot has a powerful claw with which when the animal is brought to bay it has been known to rip open a dog. The allied genus *Petrogale* includes smaller species, called Rock Wallabies, with only a short claw on the hind-foot. As their name implies, they frequent rocky regions. The so-called Kangaroo-rats, *Bettongia* and others, are nocturnal animals of small size, which live on leaves, grass, and roots, the last of which they dig up with their fore-paws.

Sub-class III. EUTHERIA.

The highest division of the Mammalia, the Eutheria, includes all the most familiar animals, Hedgehogs, Rats, Rabbits, Cats, Dogs, Lions, Tigers, Horses, Oxen, Whales, Elephants, Monkeys, up to and including Man himself. In them as in the Metatheria the egg is exceedingly small, in Man and the domestic animals for instance, it varies from $\frac{1}{120}$ to $\frac{1}{200}$ inch in diameter. The upper part of the oviduct, the Fallopian tube, is consequently narrow; the uterus is however enlarged, for the egg not only lies there a long time—called the period of gestation or pregnancy—but as it is developing into the young Mammal a special organ called the placenta is developed, which grows out and becomes interlocked with folds in the wall of the uterus. This organ is a result of an enormous development of the allantois. In Eutheria, the egg contracts an adhesion with the wall of the uterus over its whole surface, but that part of the surface against which the corrugated and richly vascular allantois impinges is covered with vascular outgrowths called villi, which fit into pits on the wall of the uterus. It is this area which is called the allantoic placenta. The rest of the surface of the egg is termed the umbilical placenta. This region is non-vascular, and through it nourishment is absorbed in Metatheria. In the lower Eutheria some nourishment is absorbed through the umbilical placenta for a considerable part of the period of pregnancy, but in the higher Eutheria it is early destroyed by an extension of the allantois round the egg. Both the membrane

covering the allantois and the lining of the uterus degenerate, allowing the blood-vessels of mother and embryo to come into close contact. The placenta becomes gorged with blood driven into it by the heart of the developing embryo, and at the same time the uterus becomes congested and loses its epithelium, so that the blood of the mother and that of the young approach very closely to each other. They are separated only by the thin outer wall of the placenta, so that nourishment diffuses from one to the other, and the blood of the embryo is oxygenated and its carbon dioxide removed by the maternal blood. So close is the connection, that when the embryo is born and passes out of the uterus, carrying

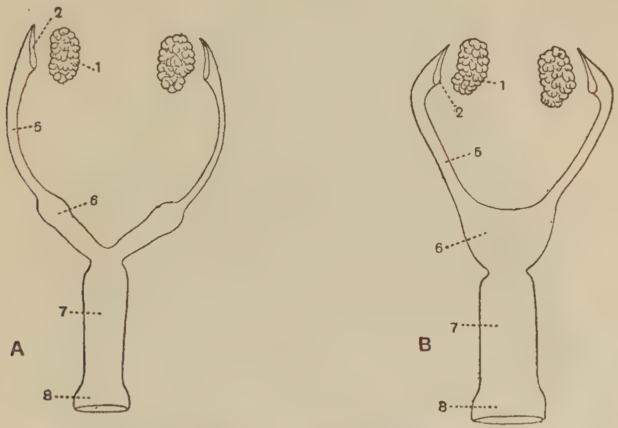

FIG. 332 Diagrams to illustrate the arrangement of the female genital ducts in an Eutherian Mammal. A. Rabbit. B. Man.

1. Ovary. 2. Oviducal funnel. 5. Fallopian tube. 6. Uterus. 7. Vagina. 8. Urino-genital sinus.

with it the placenta, the latter in most cases tears open the vessels in the wall of the uterus and the mother loses a considerable quantity of blood. The lowest parts of the two oviducts are completely joined and pass into a single passage, the vagina, while the middle portions, or uteri, are sometimes quite separate as in the Rabbit (A, Fig. 332), sometimes partly united as in the Cat, rarely completely joined as in Monkeys and Man (B, Fig. 332). In one or two Metatheria, as already mentioned, a placenta such as has been described has been recently discovered, but it is of very small extent, and does not persist until birth. These facts lead us to believe that Metatheria are degenerate descendants of early Eutheria,

and we may take as a further mark of degeneracy the almost complete disappearance of the milk set of teeth. The penis has the same structure as in Metatheria.

Order I. **Edentata.**

When we take a general survey of the orders or main divisions into which the Eutheria are divided we find that we have three or four strange groups, the relations of which to the others are most difficult to decide. These include the curious Edentata of South America, comprising three families, the BRADYPODIDAE or Sloths, the MYRMECOPHAGIDAE or American Ant-eaters, and the DASYPODIDAE or Armadillos. With these the South African forms, included in the families MANIDAE or Scaly Ant-eaters and ORYCTEROPODIDAE

FIG. 333. Tamandua Ant-eater, *Tamandua tetradactyla*. From Proc. Zool. Soc. 1871.

or Cape Ant-eaters, are usually grouped, though their relationship is a matter of doubt, and it seems clear that they have no close relationship to the South American forms, for which reason we shall use for these African families the name Effodientia. The name Edentata means "toothless," and was given to the animals of this group by the early naturalists because they supposed them to be devoid of teeth. This is only the case with one small family, the Ant-eaters, or MYRMECOPHAGIDAE, which like *Echidna*, have lost their teeth through disuse. In the rest there are teeth, but front teeth are always wanting. In the adult none of the teeth have enamel and all are similar to each other. The hands and feet are armed with great curved claws, adapted for holding on to supports, not for grasping or attacking, and

incapable of being retracted or pulled back. Consequently the hands and feet are like hooks, on which the animals walk

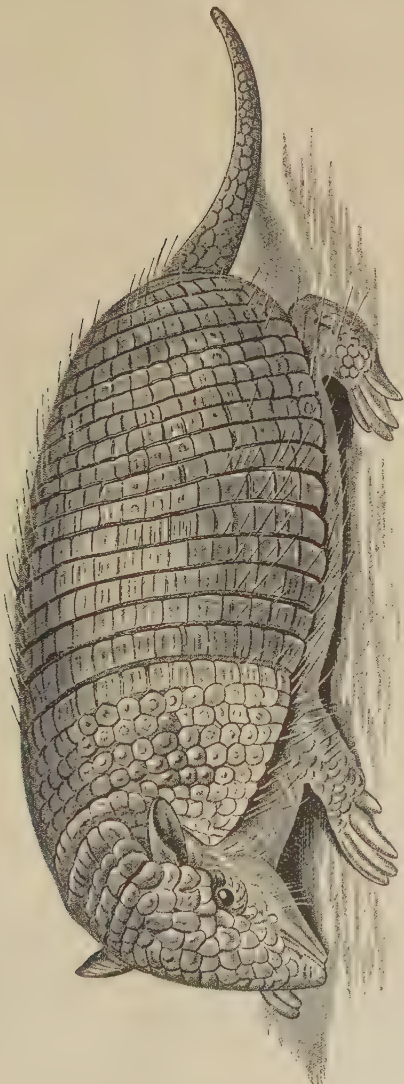

FIG. 334. The Six-banded Armadillo, *Dasypus sexcinctus*. After Vogt and Specht.

clumsily, bending the fingers under them. The apparent want of utility is however explained when the animals are looked at in

their natural surroundings. It is then seen that one family, the Sloths (BRADYPODIDAE), spend all their time climbing about on trees, on the leaves of which they feed. There is a remarkable adaptation which probably helps them to escape detection by their enemies. The surface of the hairs is grooved and affords a resting-place for a unicellular Alga which causes the animal to have a greenish appearance so as to be almost invisible amidst the foliage. The second family include the true Ant-eaters or MYRMECOPHAGIDAE; in these the strong claws are used for pulling down and digging up ant-hills. The muzzle is long and toothless. There is a very long tongue,

FIG. 335. White-bellied Pangolin, *Manis tricuspis.*

and enormous salivary glands, the sticky secretion of which entraps the ants. The Tamandua Ant-eater, *Tamandua tetradactyla*, of Central and South America, is arboreal in its habits and lives in the dense primeval forests of the New World: it uses its strong claws for climbing and has a prehensile tail. The third family, the Armadillos or DASYPODIDAE, can dig with such rapidity that a comparatively large animal will scoop out a burrow for itself in a few minutes. These Armadillos are also very remarkable as being the only Mammals in which the dermis or deeper skin develops into hard bony plates like the osteoderms of Reptilia, whilst the

hair on the upper part of the body is replaced by horny scales like those of Snakes and Lizards, covering the bony plates.

It is thought that in comparatively recent times, geologically speaking, South America was an island, and just as Australia has preserved some curious animals which could never have held their ground against the powerful Lions and Tigers and Wolves of the Old World, so also in South America evolution seems to have run a course of its own.

Order II. **Effodientia.**

The African group formerly classed with the South American Edentata consists of two genera each representative of a family and both are ant-eaters. The MANIDAE are represented by *Manis*, the Scaly Ant-eater, which has the hair agglutinated to form overlapping scales, but has no dermal plates and no teeth. This genus is also found in Eastern Asia. *M. tricuspis* is arboreal in its habits. The ORYCTEROPODIDAE are represented by the Cape Ant-eater, *Orycteropus*, which has peculiar folded teeth and scanty hair. It is termed by the Boers the Aard-vark or Earth-pig and is nocturnal in its habits, sleeping during the day in burrows which are usually found in the neighbourhood of the large ant-mounds so common on the veldt. The womb and the placenta in this group are of quite a different type from that which is found in true Edentata, and this is one of the main reasons for separating the two groups. In Edentata the two uteri have coalesced to form a single dome-shaped uterus, whereas in Effodientia the two uteri have coalesced only at their lower portions and a forked or "bicornuate" uterus is the result.

Order III. **Insectivora.**

This is a group of small animals which, as their name implies, feed chiefly on insects. They have three or four sharp pointed cusps on each of their back teeth, adapted for piercing the armour of insects, while their front teeth in both jaws are directed outwards so that they act like a pair of pincers in seizing the prey. The Insectivora are plantigrade, that is, they place the whole palm and the whole sole on the ground when they walk (Figs. 336, 337); in nearly every case they have the full number (five) of fingers and toes; they have long flexible snouts projecting beyond the mouth and their brains are of a low and simple structure, the surface of the cerebral hemispheres being smooth, while they leave the cerebellum

uncovered. In many cases there is a shallow cloaca surrounded by a sphincter into which both anus and urino-genital passage open. They possess an allantoic placenta, but this covers only a portion of the surface of the egg, the rest of the surface of the egg being occupied by an umbilical placenta. In this respect they are hardly more advanced than those Metatheria which retain an allantoic placenta. The Insectivora, as may be seen from the description, are a very primitive group, and like other primitive groups consist of a number of families widely differing from one another in structure. Taking a broad view we may say that the tropical families exhibit the highest grade of structure. Thus the GALEOPITHECIDAE, or Flying-shrews, represented by the genus *Galeopithecus*, have a parachute-like expansion of skin extending from neck to hand, forming a web including the fingers. A similar expansion of skin reaches from wrist to foot, forming a web between the toes, and there is a piece of skin connecting the two legs behind. There is a ring of bone round the orbit, and the symphysis pubis is long and strong. The TUPAIIDAE, or Tree-shrews, have likewise the orbit encircled by bone and a strong symphysis pubis, but they are devoid of any parachute-like extension of skin. They are small animals with large eyes and long furry tails; both these groups are confined to the Malay Archipelago and India and both inhabit trees.

The MACROSCELIDAE have no bony ring round the orbit but they possess a strong symphysis pubis. Their most marked characteristic is an elongated foot (see Fig. 336) which enables them to make great springs. Hence the name Jumping-shrews. They are represented by 14 species distributed over Africa.

The three families which represent the Insectivora in Great Britain are all of a lower type. Not only is the orbit never surrounded by bone but the zygomatic arch is slender and sometimes even absent. The brain cavity is very small and the symphysis pubis is very short; sometimes the pubes are united only by ligament.

The first of these families is the ERINACEIDAE, or Hedgehogs, distinguished by the slender zygomatic arch, and by the tympanic being in the form of a ring. The well-known Hedgehog, *Erinaceus europaeus*, is intermediate in size between a rat and a rabbit. It has the fur intermixed with spines, and when alarmed can roll itself into a ball, tucking in head, limbs and tail, and in this condition can bid defiance to its enemies. All Erinaceidae are not of this character; the rat-like *Gymnura* from India and the Malay Peninsula is without spines.

The other two families are the Shrew-mice (SORICIDAE) and the Moles (TALPIDAE); these are represented in both Great Britain and North America, but the latter country is without Hedgehogs. The Soricidae have lost the zygomatic arch altogether, the pubes are disconnected and the tympanic is ring-like. As the popular name implies these are mouse-like animals covered with fur. There are three British species, *Sorex vulgaris*, about the size of an ordinary Mouse, *Sorex pygmaeus*, one of the smallest Mammals known, and *Crossopus fodiens*, the Water-shrew, distinguished by

FIG. 336. African Jumping-shrew, *Macroscelides tetradactylus* × ½. From Peters.

having the feet frayed with stiff hairs to aid in swimming. The North American *Blarina* has the aspect of a Mole with its small eyes and rudimentary outer ears. It is called the Mole-shrew, but its normal arms and hands at once distinguish it from the true Moles. The true Moles, TALPIDAE, are above all characterised by the greatly enlarged hands and powerful though short arms by which they are adapted for a burrowing life. To make room for the large hands in narrow burrows the front segment of the sternum is greatly elongated, thus carrying the pectoral girdle and limbs forward

on to the neck, where there is room for them. The clavicles are short, almost square bones, and the humerus of the arm is short and stout. The zygomatic arch is present and the tympanic is a bulla. The TALPIDAE are represented in Great Britain by *Talpa europaea*, the Common Mole, which feeds on earthworms, constructing a complicated system of underground passages through which it hunts its prey. In North America the commonest is perhaps *Condylura cristata*, the Star-nosed Mole, the snout of which is encircled by a ring of fleshy outgrowths.

The Russian Desman, *Myogale moschata*, belongs to the Mole family once extended as far west as Britain. It lives in burrows by the water-side and feeds chiefly on fresh-water insects and their larvae. In correspondence with its mode of life the hind-feet are webbed and the tail large and compressed, forming an efficient swimming organ. It is hunted for its fur (Fig. 337).

There still remain four families to be mentioned, each of which however is represented by a few species. These are interesting because, (1) they have a more primitive type of molar tooth than any other living Mammals; (2) in their distribution, like the ancient genus *Peripatus*, they belong to the Southern Hemisphere, only overstepping it when they go into the West Indies. The type of tooth is the tri-tubercular, which is found in the oldest remains of Mammals known: it is distinguished by the reduction of the characteristic cusps of the insectivoran tooth to three which form the points of a triangle. Of these primitive families the (1) CHRYSOCHLORIDAE are the Golden Moles of the Cape, so-called from the iridescent sheen of the fur. They have the reduced eye and enlarged hands and arms of the ordinary Mole, but these hands and arms are placed not at the sides of the neck but at the sides of the thorax, the ribs of which are bent inwards to create hollows for their reception. The zygomatic arch is present and the tympanic is a bulla. The remaining families have lost the zygomatic arch and the tympanic is a mere ring. These are (2) POTAMOGALIDAE, represented by a single species, Water-shrews from Central Africa with a flattened tail, short limbs and no clavicles, (3) SOLENODONTIDAE, and (4) CENTETIDAE, two externally similar but not closely allied families of small hog-like animals with stout limbs, the first from Cuba and Hayti and the second from Madagascar.

The most interesting circumstance about the Insectivora is the fact that when by means of fossils we trace back the higher groups of Mammals they seem all to merge imperceptibly into forms which from their teeth and general organisation we should class as

Insectivora. There is therefore really good ground for supposing that the living Insectivora, though modified in special details, nevertheless represent, so far as their general organisation is concerned, the earliest type of Eutheria which appeared on the globe. From these original Insectivores advance seems to have taken place along four lines:—(I) some Insectivora took to attacking larger prey, including their own less fortunate relatives, and gradually developed into the Carnivora or flesh-eating Mammals: (II) some became vegetable

FIG. 337. Russian Desman, *Myogale moschata.*

feeders and gave rise to the great group of hoofed animals, relying either on their swiftness or on their size and strength for defence: (III) some took to burrowing and developed into gnawers or Rodents, relying chiefly on their burrows for safety: (IV) some took to climbing trees when hard pressed, and of these some (*a*) developed the power of leaping from tree to tree into the power of flying, the fore-limb becoming changed into a wing; these are the Bats; the rest (*b*) remained purely tree dwellers, and eventually gave rise to the great group of the Primates which includes Monkey and Man.

Order IV. Carnivora.

The Carnivora are distinguished above all by their teeth (Fig. 317). They have small insignificant front teeth or incisors, but the eye-teeth or canines, situated in the maxilla just where it meets the premaxilla, are large and pointed. With these the animal seizes and kills its prey. The premolars have cutting edges, consisting typically of a large central cusp and two smaller ones, one in front and one behind. The molars with the exception noted below are broad and crushing (Figs. 317 and 338). The last premolar in the upper jaw and the first molar in the lower jaw constitute what are called the carnassial teeth. These are very large blade-like teeth which bite on one another like a pair of scissors. The upper one has enlarged central and posterior cusps, the anterior cusp being small or wanting; the lower carnassial has an anterior blade-like portion consisting of two cusps and a posterior flattened portion or heel. The nails are sharp curved claws.

The most familiar examples of this class of animals are our Dogs and Cats. The wild ancestors of the domesticated pets are unknown, though the Dog's ancestors were no doubt allied to the Wolf, whereas the Cat is probably descended from some species belonging to the East, allied to but distinct from the Wild Cat, *Felis catus*, still found in remote parts of Scotland and possibly in the mountains of North Wales. Possibly the Domestic Cat has originated from the Caffre Cat, *F. caffra*, which extends throughout Africa and was considered sacred by the ancient Egyptians, who embalmed their bodies in such amazing numbers that their mummies have been exported from Egypt and used as manure.

In the Dog, *Canis familiaris*, and the other members of the family CANIDAE, the muzzle is long and the teeth numerous. Their arrangement can be expressed by the dental formula i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{4}$ m. $\frac{2}{3} = 42$, where the upper line shows the teeth in the upper jaw, the under line those in the lower. The first figure denotes incisors, the second canines, the third premolars and the last molars. The hindermost back teeth, or molars, are still broad. The fore-legs cannot be used for grasping. The claws are comparatively blunt and cannot be retracted.

In the domesticated Cat, which is a typical member of the Family Felidae, on the other hand the muzzle is short, and the

teeth reduced in number, the formula being i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{3}{2}$, m. $\frac{1}{1} = 30$, whilst the fore-limbs can be used for seizing. The claws are very sharp, and can, when not in use, be completely retracted or rather raised, so as not to wear the points. In all these

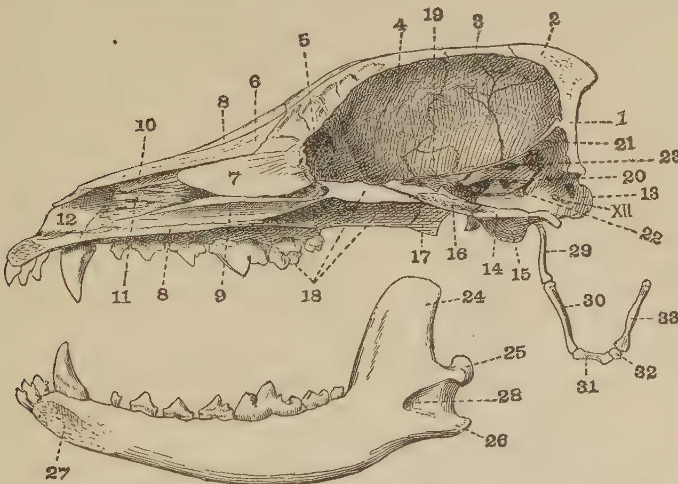

FIG. 338. Vertical longitudinal section taken a little to the left of the middle line through the skull of a Dog, *Canis familiaris* × ⅘.

1. Supra-occipital. 2. Interparietal. 3. Parietal. 4. Frontal. 5. Cribriform plate. 6. Nasal. 7. Mesethmoid. 8. Maxilla. 9. Vomer. 10. Ethmoturbinal. 11. Maxilloturbinal. 12. Premaxilla. 13. Occipital condyle. 14. Basi-occipital. 15. Tympanic bulla. 16. Basisphenoid. 17. Pterygoid. 18. Palatine. 19. Alisphenoid. 20. Internal auditory meatus, the passage for the eighth nerve to the internal ear. 21. Tentorium, a fold of calcified connective tissue projecting into the cranial cavity and separating the cerebrum from the cerebellum. 22. Foramen lacerum posterius, the passage for the tenth nerve. 23. Floccular fossa, the cavity in which the floccular lobe of the cerebellum is lodged. 24. Coronoid process. 25. Condyle. 26. Angle. 27. Mandibular symphysis. 28. Inferior dental foramen. 29—31. Segments of the second visceral arch. 29. Stylohyal. 30. Epihyal. 31. Ceratohyal. 32. Basihyal. 33. Thyrohyal, the third visceral arch. XII. Condylar foramen, the aperture through which the twelfth cranial nerve leaves the skull.

respects Cats are more perfectly adapted for a carnivorous life than Dogs, since these latter still retain traces of their descent from a different kind of Mammal. Just as the Wolf, *C. lupus*, the Jackal, *C. aureus*, and the Fox, *C. vulpes*—the last-named the only wild species of *Canis* found in Britain—are species of Dogs distinguished from each other by size and slight peculiarities of hair, etc., so the

Lion, *F. leo*, the Tiger, *F. tigris*, the Leopard or Panther, *F. pardus*, the Lynx, *F. lynx*, and the Puma, *F. concolor* (frequently called a "Panther" in America, where it is found from Canada to Patagonia), are all Cats. The differences in the colour of the skin which help to distinguish them are in all probability due to the fact that the colours are protective, enabling the animals when in their natural surroundings to escape the notice of their prey. Thus Lions, which as a rule live in dry and rather open places, are of dun colour; the stripes of the Tiger's skin deceptively resemble the alternating shadows and sunlit strips of ground found amongst the reeds in which it lives; the spots of the Leopard are undiscoverable amidst the alternating patches of light and shade caused by the sunlight struggling through the interstices of the foliage of a forest.

The Bears, URSIDAE, represent a third type of Carnivora. They are plantigrade, placing the whole sole of the foot on the ground; the molars are blunter than those of the Cats and Dogs and very broad, the carnassials are broad and the premolars very small and often fall out; the upper carnassial is a comparatively small tooth and the heel of the lower carnassial is larger than the blade; these peculiarities are connected with the fact that the Bears are not merely flesh feeders but can live partly on a vegetable diet. The Brown Bear of Europe, *Ursus arctos*, which used to be abundant in Britain, is so nearly allied to the Grizzly Bear, *U. horribilis*, of the Rocky Mountains, that the latter is by some authorities placed in the former species. In Eastern Canada, especially in the Province of Quebec, the Black Bear, *Ursus americanus*, is very abundant and is trapped for its fur. It is usually an inoffensive animal, feeding on berries and bark, but occasionally, especially when it has cubs, it will attack man. The remains of fossil Carnivora demonstrate that the Ursidae were derived from primitive types of Canidae in the Miocene period.

The Stoats, Weasels, Martens, Minks, Polecats, Otters, Badgers and Skunks, forming the family MUSTELIDAE, are sometimes supposed to be allied to the Bears, but are really very distinct. They have very long necks, slender, flexible bodies and short limbs, and their habits are exceedingly bloodthirsty and ferocious. The chief resemblances to Bears are found in the skull and teeth, but the contrast in general build and in gait (the Mustelidae are digitigrade) is very striking. Six species of Mustelidae are found in Great Britain: (1) The Otter, *Lutra vulgaris*, an animal which has webbed toes and a long, somewhat flattened tail. It lives on fish, passing much of its time in the

water. (2) The Badger, *Meles taxus*, a heavy, somewhat clumsy animal with blunt claws and short limbs, leading a nocturnal, burrowing life and feeding on mice, reptiles, insects, fruit, acorns and roots. (3) The Pine Marten, *Mustela martes*. (4) The Polecat, *Putorius foetidus*, which feeds on small mammals, birds, reptiles and eggs, and has a disagreeable odour. The Ferret is a domesticated variety of the Polecat. (5) The Weasel, *Putorius vulgaris*. In cold regions the Weasel turns white in winter. (6) The Stoat, *Putorius ermineus*, which also turns white in cold climates except the tip of its tail, which remains black. Its winter fur is much prized and is

FIG. 339. The Common Skunk, *Mephitis mephitica*.

termed Ermine. These last four are closely related species with long, slender bodies, sharp curved claws and ferocious habits.

In North America there is an interesting family, the PROCYONIDAE, intermediate between the Ursidae and Mustelidae. The members of this family have sharp muzzles but clumsy bodies and short necks; the Raccoon, *Procyon lotor*, is the most familiar. It is omnivorous. The Mustelidae are represented by Otters, Martens and a remarkable form, the Skunk, *Mephitis mephitica* (Fig. 339), which produces a secretion of such repulsive odour as to make it

avoided by other animals and a terror to man. It is strikingly marked with sharply contrasted black and white patches but these alternations of shade tend to conceal it by breaking up its outline as seen in the pale moonlight when it sallies forth to seek its prey. The VIVERRIDAE should be mentioned although they are a tropical group. In general shape they resemble the Mustelidae, but in the shape of the carnassial teeth and in the division of the auditory bulla by a septum they agree with the Felidae. The best-known members of the family are the African and Indian Civet Cats (*Viverra civetta* and *V. zibetha*) from whose perineal glands the civet of commerce is obtained. Fossil remains connect the Viverridae and Mustelidae and one would not be far astray in calling them "Primitive Cats."

The Carnivora mentioned hitherto are often grouped together as the *CARNIVORA VERA* or *FISSIPEDIA*. The second group of recent Carnivora is represented by the seals and is termed the *PINNIPEDIA*. The name is derived from the fact that fingers and toes are united by webs of skin. The Seals are almost as purely marine animals as the Whales and Sea-cows, but they have become adapted to their surroundings in quite a different way. Thus their fur is close and thick, and they are protected against the cold of the water by it, instead of being covered all over by a thick layer of fat as are the Whales. The tail is short and insignificant, but they make a powerful stern oar by directing the feet backwards parallel to the body so that the soles are turned up. Thus the feet act just in the same way as the tail does in a Whale, making up and down strokes and driving the animal forward. The whole upper part of the limb is buried in the body. In one group, the true Eared or Seal-skin Seals, OTARIIDAE (the fur of some species of which is used for making jackets), the feet can be turned forward when the animal comes on land. There are also some traces of an external ear, whence comes the name OTARIIDAE or Eared Seals which is given to them. They are confined to the Pacific coasts of America and Asia. Species termed "Sea-lion" (*Otaria jubata*) thrive well in captivity, and are often seen in Zoological Gardens (Fig. 340). The Walrus, *Trichechus rosmarus*, of the Arctic seas, is the representative of a second family, the TRICHECHIDAE. No external ear is present but here also the feet can be turned forward. The canine teeth of the upper jaw are very long and give the animal a fierce appearance. They are however chiefly used for digging up bivalves from the mud and for climbing on the blocks of ice in the Arctic regions where the animal is found. The name "Old Man"

sometimes given to it by whalers is suggested by the tufts of gray hair on the sides of the face. The common Greenland Seal, *Phoca vitulina* and the Gray Seal *Halichoerus grypus*, both of which are found round the British coasts in out-of-the-way places, belong to the third family PHOCIDAE, the members of which are distinguished by having no ear-flaps and by being unable to turn their feet forwards. For this reason when they are on land they can only move by wriggling on their abdomens aided by movements of the fore-limbs. *Phoca vitulina* is common on the eastern coasts of Canada and the United States of America.

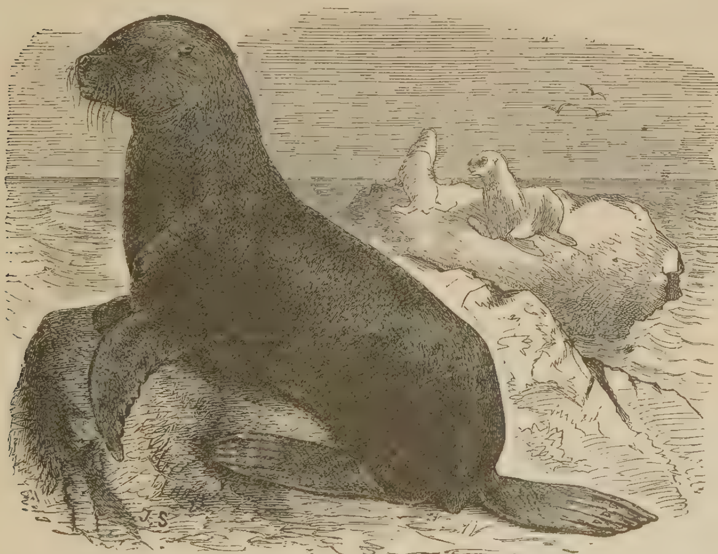

FIG. 340. The Patagonian Sea-Lion, *Otaria jubata*. From Sclater.

Order V. Cetacea.

The order of Whales includes Mammals thoroughly adapted to an aquatic life which pass all their life in the water. The great majority of them are confined to the sea but a few are found in the great rivers. In consequence of their mode of life they have undergone great changes of structure. Thus all external trace of the hind-limbs has disappeared although a pair of small bones representing the pelvic girdle are found embedded in the body. The fore-limbs have become flippers. The fingers are bound together by skin to their very tips and the number of joints (phalanges) in each

finger has been greatly increased; the limb is buried in the body almost to the wrist. The terminal vertebrae of the tail have become flattened and have expanded transverse processes (diapophyses). These support a flattened tail fin which is extended in the horizontal plane not in the vertical plane like that of true Fish. Whales progress by moving the tail fin up and down, whereas in Fish the movement is from side to side.

All hair has disappeared, only one or two hairs being found in the region of the lips in the embryo and these disappear when the adult state is reached.

The body is covered with a thick layer of fat termed blubber, which preserves the heat of the body and thus in a different way the Whale is as well protected against the cold water as is a Seal which has retained its thick furry coat. It is for the sake of the blubber which is used for making oil that Whales are principally hunted now-a-days. The skull is distinguished by the great rounded cranium and by the elongation of the bones of the face and jaws. These support an immense prow-like snout formed chiefly of fat, which is an admirable buttress of defence for the animal's skull. The supra-occipital bone is of great size and forms the posterior surface of the cranial dome, interposing between the small parietals and meeting the frontals. The frontals develop great orbital plates flanking the face, beneath which is the small orbit bounded below by the slender jugal. The nasal organ has almost totally disappeared: the vestigial nasal bones overhang an almost vertical air passage which leads from the choanae to the external nares. These latter open by a single opening termed the blow-hole placed far back on the upper surface of the head. The epiglottis and the arytenoid cartilages surrounding the glottis are prolonged upwards into a kind of cone which is tightly embraced by a downward prolongation of the soft palate: and thus the mouth can be opened widely and enormous quantities of water taken into it, whilst all the time air can pass uninterruptedly from the blow-hole to the lungs and *vice versâ*. When a Whale rises to the surface to breathe, it empties its lungs by a strong blast just before it actually reaches the surface, and in this way an ascending column of hot moist air is produced. The moisture rapidly condenses into water, the column seen from the deck of a ship looks like a jet of sea-water, and in common parlance the Whale is said to "spout." In Whales also the teats are situated far back, as they are in Cows, and the connection of larynx and soft palate which enables the adult to

breathe and eat at the same time enables the mother Whale to force milk down the young one's throat without choking it.

It is an interesting fact that the nasal organ should have become vestigial in Whales whereas in Fish, it is a large and important sense organ. But we must remember that the nasal organ was originally evolved for the purpose of perceiving substances dissolved in water: but that when land animals were evolved from Fish this organ became adapted to perceive gaseous substances in the air which was drawn past the opening of the nasal organ. Now the Whale is interested in substances dissolved in the water, not in gaseous odours in the air, but as an air-breathing animal it could not admit water to its nasal organ without the risk of choking, and hence this organ has lost its function and become vestigial.

The external ear is liable to become a great nuisance to an animal which spends so much of its time beneath the surface of the water as every swimmer and diver knows to his cost. Hence in Whales it is reduced to capillary dimensions so as to exclude the water as much as possible. In a Porpoise six feet long, it is of the dimensions of a pin hole. It is certain therefore that Whales do not hear through the outer ear: they hear through the bones of the head as a fish does. This point was made clear by experiments designed to find out the best means of detecting a submerged submarine.

Whales are divided into sub-orders, the whalebone Whales or *MYSTACOCETI* and the toothed Whales or *ODONTOCETI*. In the latter there are numerous teeth, but they are all alike and simple (Fig. 341), and the maxilla develops a great crest which conceals the orbital plate of the frontal. The great Sperm-whale, *Physeter macrocephalus*, of the Southern Seas, has teeth only in the lower jaw and feeds on cuttle-fish and fishes, gripping the long flexible arms of the former by pressing them against the upper jaw. Spermaceti oil is the melted-down fat of this monster. The Ca'ing or Pilot Whale (*Globicephalus melas*), which also feeds chiefly on cuttle-fish, has teeth on both upper and lower jaws (Fig. 341). Pilot-whales are social in disposition, and the herds are occasionally driven into bays or fiords in the North Atlantic and captured. Smaller toothed Whales are found round the coast of Britain which have teeth in both jaws. Of these we may name the Porpoise, *Phocaena*, the Dolphin, *Delphinus*, and the Grampus, *Orca*. The common Porpoise, *Ph. communis*, is the most abundant and best known of British Cetaceans. It is not more than six feet long and is often cast ashore. It abounds in the Firth of Clyde. In the Gulf of St Lawrence the White Whale, *Delphinapterus leucas*, is fairly common. It attains a length of twelve feet.

The whalebone Whales, Mystacoceti, have no teeth. The orbital plate of the frontal is uncovered and there is a small ethmoturbinal covered with olfactory epithelium. They are all large animals, although they feed on the smallest prey, such as minute pelagic mollusca, jelly-fish and crustacea. The "whale-

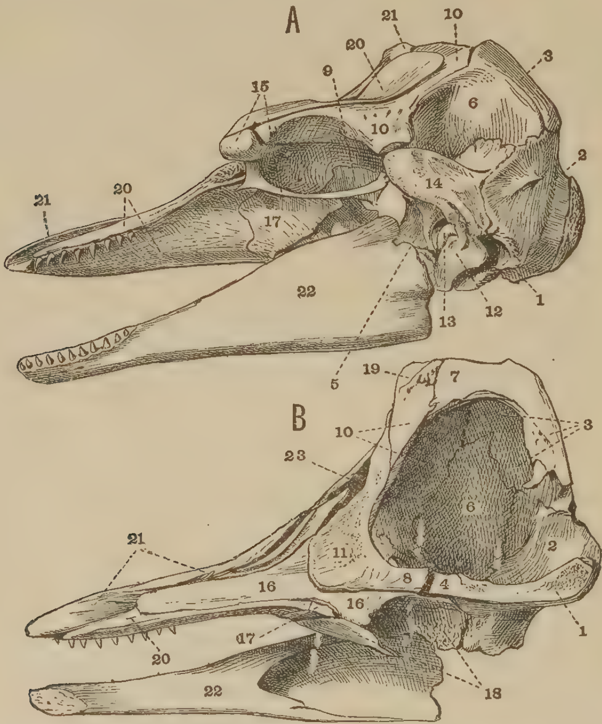

FIG. 341. A. lateral view, and B. longitudinal section of the skull of a young Ca'ing Whale, *Globicephalus melas* × $\frac{1}{8}$.

1. Basi-occipital. 2. Exoccipital. 3. Supra-occipital. 4. Basisphenoid. 5. Alisphenoid. 6. Parietal. 7. Interparietal fused with 3. 8. Presphenoid. 9. Orbitosphenoid. 10. Frontal. 11. Mesethmoid. 12. Tympanic. 13. Periotic. 14. Squamosal. 15. Jugal. 16. Vomer. 17. Palatine. 18. Pterygoid. 19. Nasal. 20. Maxilla. 21. Premaxilla. 22. Mandible. 23. Anterior nares.

bone" or baleen consists of a large number of horny plates hanging down like curtains from the palate into the cavity of the mouth. These are placed in pairs, one on each side of the mouth, one pair behind the other, and the fellows of a pair nearly meet in the middle. The lower edges of these plates are frayed out so as to form a fringe

or strainer. After the Whale has taken water into its mouth it raises its tongue against the edges of the plates and allows the water to trickle out through the strainer described above; all the small animals taken in the water are thus retained and then swallowed. The best quality of whalebone is obtained from the Right Whale, *Balaena mysticetus*, an animal about 50 feet long, found only in the Arctic regions. The Great Rorqual Whale, *Balaenoptera sibbaldi*, has a fin in the middle of its back, and attains a length of 60—80 feet; it is the largest animal now found on the globe and is very abundant. The Lesser Rorqual, *Balaenoptera rostrata*, is a smaller animal some 30 feet in length. On two occasions at least the animal has strayed up the St Lawrence as far as Montreal where it has been starved to death in fresh water. The head of *Balaenoptera* is much shorter than *Balaena* and the whalebone is shorter and coarser.

In Eocene deposits remains of primitive toothed Whales are found which have been termed "Zeuglodonts," because the teeth have two distinct roots and were at first mistaken for two teeth fused together, hence the name (Gr. ζεύγλη, loop of a yoke; ὀδούς, ὀδόντες, teeth, lit. yoked-teeth). The teeth were distinguishable into incisors, canines and trenchant cheek-teeth like the premolars of the Dog. These remains give reason to believe that the land-mammal from which Cetaceans were derived was a member of the group Creodonta—an extinct group which might be described either as primitive Carnivora or as intermediate between Insectivora and Carnivora. This group was distinguished by the possession of small incisors, large canines and trenchant cheek-teeth carrying three cusps like those of primitive Insectivora but no carnassial teeth were differentiated. It is quite possible that Seals (Carnivora Pinnipedia) are likewise directly derived from Creodonta since they also have no carnassial teeth. In this case Whales and Seals would represent two independent adaptations of primitive Carnivora to aquatic life, but the means by which the adaptation was effected are totally different in the two cases, for the hairy coat of Seals is functionally replaced by the blubber of Whales whilst the powerful tail fin of Whales is represented by the hind-legs of Seals.

Order VI. **Ungulata.**

The great group of the Ungulata or hoofed animals represents the second line of evolution from the primitive Insectivora. Here we find that all power of grasping with the limbs is absent and the

feet are purely adapted for running, the toes being encased in hard blunt nails which are called hoofs. At the present time the Ungulata include a number of very diverse forms. But it must be remembered that a large proportion of the group is extinct, and that to some extent the fossil forms serve to connect the very heterogeneous members of the group that still exist.

Sub-order 1. **Sub-ungulata.**

In former times there existed a great assemblage of big and often clumsy animals belonging to the Ungulata in which the toes were all nearly equal in length and the bones of the wrist arranged in parallel longitudinal series. The Sub-ungulata at one time spread over the earth and in South America, which became isolated in early times, they gave rise to a great variety of forms. Some of these mimicked the members of the other sub-order of the Ungulata, and formed one of the most striking examples of parallel evolution. Only two families of the *SUB-UNGULATA*, as these animals are called, survive at the present day. These are the family of the *Hyrax*, HYRACIDAE, and the Elephant family, PROBOSCIDEAE.

HYRACIDAE.

Family Hyracidae.

The *Hyrax* (*Procavia*) is the Coney mentioned in the Bible. The Hyracidae are small, not unlike rabbits in appearance, but their hind-feet closely resemble those of the Rhinoceros. Their front teeth are, it is true, somewhat chisel-shaped, as in the Rodentia, but there are four of these below and two above, which is quite unlike the arrangement in the rabbit. It is possible however that the two teeth reckoned as lower posterior incisors may really be canines, since they do not, like the other incisors and like those of the Rabbits, grow throughout life (Fig. 342). These animals are found throughout Africa except in the north and also in Arabia and Syria. Only one genus is now recognised, *Hyrax* (*Procavia*), with several species. Most of these live amongst rocks, in mountains and in stony places, but some frequent the trunks and large branches of trees and sleep in holes.

PROBOSCIDEAE.

Family Proboscideae.

The Elephant is too well known to need much description, but it may be pointed out that its trunk is really a long flexible snout, an excessive exaggeration of what is found in Insectivores, and that its tusks are front teeth, only

those in the upper jaw being developed, and finally that the upper parts of the arms and legs are quite free from the body, instead of being, as is usually the case with Mammals, buried inside the general contour of the body. There are only two living species, the African Elephant, *Elephas africanus*, inhabiting the forest region of tropical Africa and hunted for its tusks, and the Indian Elephant, *Elephas indicus*, inhabiting the jungles of India, Further India, Ceylon and Sumatra, which is frequently domesticated. The canines are lost and have left no traces. The molars succeed one another in a horizontal row, never more than two being at any one time functional (Fig. 343). The ridges on these teeth when worn present the appearance of parallel bands in the Indian Elephant, but in the African

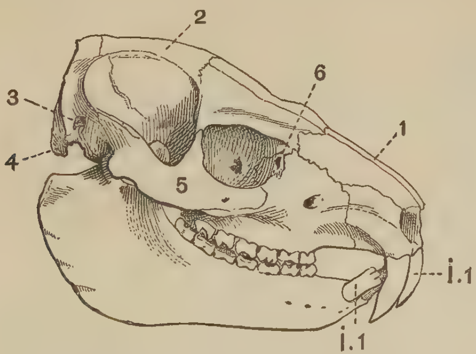

FIG. 342. Skull of *Hyrax* (*Procavia*) *dorsalis* × $\frac{2}{3}$.

1. Nasal. 2. Parietal. 3. External auditory meatus. 4. Process of the exoccipital. 5. Jugal. 6. Lachrymal foramen. i 1. First incisor.

they form diamond-shaped lozenges. The ears of the latter species are very large and the trunk ends in two nearly equal prehensile "lips" attached to its lower margin. In the Indian Elephant the ears are smaller; there is but one finger-like "lip" at the end of the trunk and this is attached to the upper margin of the trunk. The skull is very massive, but the exterior gives an erroneous impression of the size of the brain-case because the bones are enormously thickened and contain large air-spaces, especially in older specimens, where the frontals may attain a thickness of one foot. The evolution of the Elephant from an ordinary type of pig-like animal has been elucidated by the labours of Dr Andrews. In the Glacial Period which immediately preceded the one in which we are living, a hairy Elephant the Mammoth (*Elephas primigenius*)

roamed over Northern Europe and Asia and was hunted by primitive man. In older deposits we come on the remains of Elephants known as *Stegodon* and *Mastodon* in which the ridges crossing the molars of Elephants reveal their character by breaking up into pointed cusps like those on the teeth of Insectivores. In the earlier species of *Mastodon* a rudimentary pair of lower incisors is present in addition to the tusks. In Miocene deposits remains of a creature termed *Tetrabelodon* are found in which there was only a short trunk, but which possessed a pair of long lower incisors in addition to the

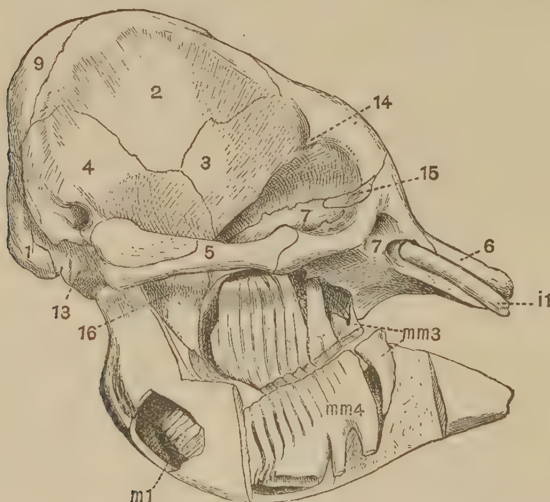

FIG. 343. Skull of a young Indian Elephant, *Elephas indicus*, seen from the right side, the roots of the teeth have been exposed × ⅛.

1. Exoccipital. 2. Parietal. 3. Frontal. 4. Squamosal. 5. Jugal. 6. Premaxilla. 7. Maxilla. 9. Supra-occipital. 13. Basi-occipital. 14. Postorbital process of the frontal. 15. Lachrymal. 16. Pterygoid process of the alisphenoid. i 1. Incisor. mm 3, mm 4. Third and fourth milk molars. m 1. First molar.

upper tusks. In the contemporaneous *Dinotherium* these lower incisors formed downwardly curved tusks and the upper incisors were absent. The animal could not have used these inwardly curved incisors for offence but must have used them for grubbing up roots. Finally in the Eocene period a beast is found with comparatively short upper and lower incisors and the trunk was not better developed than it is in Insectivora. It adds to the interest of these discoveries to know that the remains of all this ancestral

chain of animals are found in the same region (N. Africa) in deposits lying directly above one another. Dr Andrews seems to have discovered the actual locality where the evolution of the Elephant occurred, a discovery which it has fallen to the lot of few to make.

Sub-order 2. **Ungulata vera.**

All the rest of the Ungulata have the thigh and the upper arm more or less buried in the body, whilst the heel and the wrist are raised in walking so that the creature goes along on the tips of its

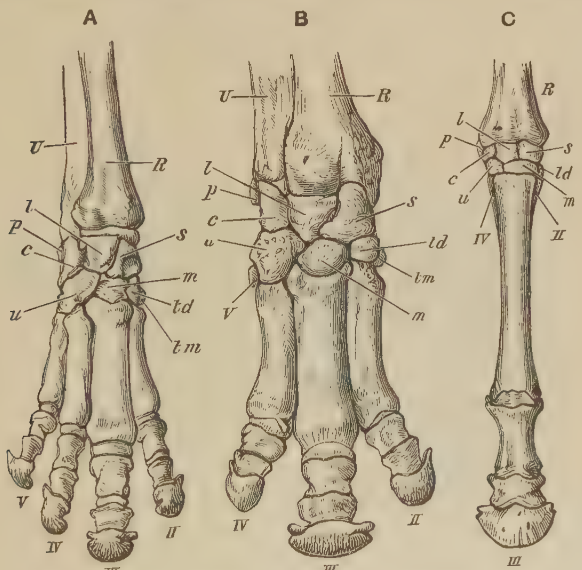

FIG. 344. Bones of right fore-foot of existing *Perissodactyles*. A, Tapir, *Tapirus indicus* × ⅕. B, Rhinoceros, *Rhinoceros sumatrensis* × ⅕. C, Horse, *Equus caballus* × ⅛.

c. Cuneiform (ulnare). *l.* Lunar (intermedium). *m.* Magnum (third distal carpal). *p.* Pisiform. *R.* Radius. *s.* Scaphoid (radiale). *td.* Trapezoid (second distal carpal). *tm.* Trapezium (first distal carpal). *U.* Ulna. *u.* Unciform (conjoined 4th and 5th distal carpals). II—V, second to fifth digit. From Flower.

toes. The bones of the wrist are arranged in transverse rows, the members of two adjacent rows alternating with one another. The first digit in both fore- and hind-limbs is entirely absent. These true Ungulates, *UNGULATA VERA*, as they are called, are divided into two great groups: (1) the *PERISSODACTYLA*, in which there is an odd number of toes and in which the true central axis of both

arm and leg runs down through the centre of the third finger or toe (Fig. 344), and (2) the *ARTIODACTYLA*, in which there is an even number of toes, and in which the axis of the limb passes down between the third and fourth toes (Fig. 347).

Division I. *PERISSODACTYLA.*

The Perissodactyla were formerly a numerous class of animals, but now three families alone survive, the Tapirs, TAPIRIDAE; the various species of Rhinoceros, RHINOCEROTIDAE; and the Horse and numerous species of Ass, EQUIDAE.

Tapiridae.

Of these the oldest and most primitive are the TAPIRIDAE. They still have four toes on the fore-feet, which is an even number; but as they have only three on the hind-feet and in both fore- and hind-feet the axis of the limb runs through the third toe, there is no doubt that they are to be classed with the Perissodactyla (Fig. 344). The snout is long and flexible, longer than the snout of the Insectivores but not so long as the snout of the Elephant. A most interesting feature in the natural history of the Tapirs is that they are now found only in two widely separated parts of the world, viz., the north of South America and in the Malay Peninsula with the neighbouring islands of Borneo and Sumatra. We need not however suppose that there was at one time a land bridge across the Pacific, for in Eocene rocks we find remains of Tapirs all over Europe, Asia and America, so that the present species are to be regarded as two separated remnants of a great race of animals which once had a very wide distribution. Their present range affords an often quoted example of what is known as "discontinuous distribution."

Rhinocerotidae.

The RHINOCEROTIDAE are represented at the present day by the genus *Rhinoceros.* The Rhinoceros is a heavier and clumsier animal than the Tapir; it has three toes on both fore- and hind-feet and no projecting snout. Its chief peculiarity however is the horn which it carries so to speak on the bridge of its nose. The horn has no bony core, and as it is entirely composed of horny matter may be said to be a mass of hairs stuck together. There are several species found in Asia and in Africa; the best known is perhaps the Indian, *R. unicornis* (Fig. 345); the Javan, *R. sondaicus*, is smaller. Both these species have but one horn. Two-horned Rhinoceroses (the two horns standing one behind the other) are now found in the Malay Peninsula,

Borneo and in Sumatra (*R. sumatrensis*), while in Africa there are several species; the commonest, *R. bicornis*, is frequently shown in menageries. It is supposed that the idea of the unicorn was derived from the one-horned Rhinoceros, but if this be so the imagination must have played a powerful part in evolving the graceful animal which figures in the royal arms out of the clumsy Rhinoceros.

Equidae.

The general appearance of the Horse, *Equus caballus*, is sufficiently well known, but the structure of its feet, which, next to the wings are the most highly specialised organs of locomotion in the animal kingdom, demand careful attention.

FIG. 345. Indian Rhinoceros, *Rhinoceros unicornis*. From Wolf.

The apparent "knees" of the Horse correspond to the joints of the wrist and the ankle, the true elbow and knees are concealed in the body of the animal, although the motion of these joints can be clearly seen if a running Horse be watched. A Horse walks on the very points of its finger and toe-nails, and it possesses only one finger on each hand and one toe on each foot (C, Fig. 344), the fingers and toes corresponding to the outer fingers, the toes of the Rhinoceros being represented merely by bones entirely concealed beneath the skin and applied like splints to the great middle finger and toe respectively. Thus the whole limb instead of being a loosely jointed flexible organ for grasping, becomes a firmly jointed lever bending only in one plane and suitable for quick locomotion.

The Horse, as we know it, has been domesticated and bred by man for thousands of years and is doubtless very unlike its wild ancestor, but there is some evidence that this wild ancestor still exists as *Equus przewalskii*, a small species of Horse with large head and bristly mane, which still roams over the steppes of Central Asia. An excellent specimen of this species could formerly be seen by visitors to the London Zoological Gardens. It showed a considerable resemblance not only to pictures of Horses found on remnants of ancient pottery but to existing breeds of Horse found in isolated parts of Northern Europe, such as the Icelandic Pony and the "Hest" of Western Norway. It had a peculiar tail which consists of a bushy wisp of comparatively short hairs as in the modern Horse; but from the centre of this bunch a tassel of very long hairs hangs down. Rude drawings of Horses with tails just like this are found on the flint tools of early man. The Zebras and Wild Donkeys have longer ears than the Horse, and they are all more or less striped; they have not got the peculiar wisp-like tail of the Horse. Such animals are found in Africa on the great plains in the south, in the deserts of Syria and Persia and in the central plains of India. Another African form, the Quagga, has become extinct in recent times. In America when discovered there were no Horses, although the Horse has since run wild there; but in the most recent geological period the Horse abounded in America and why it should have died out in a country which afterwards proved to be well suited for it is a mystery. In the same country in the deposits formed on ancient alluvial plains are found the remains of a series of animals which form a complete chain from a true Horse which appears in the newest deposits to animals which are like Tapirs but which are even more primitive since they retain a vestige of the thumb on the hand and a trace of a fourth toe in the foot. This series of forms is one of the most complete evidences of evolution known to geologists, and it seems clear that the evolution of the Horse must have taken place in this part of America.

Division II. *ARTIODACTYLA.*

Unlike the Perissodactyla, the Artiodactyla or even-toed Ungulates constitute an immense assemblage of animals, and until the invention of modern fire-arms they were the dominant animals on

the great plains of Africa and also of North America. The Artiodactyla may be divided into a higher and a lower section.

Suinae.

The lower section may broadly be called the Pigs, *SUINA*. They retain four toes on fore- and hind-feet, have a snout ending in a round flat surface and are all gross feeders, eating not only roots of various kinds but also small animals if they come in their way. Their teeth are covered with tubercles a good deal blunter than the cusps on the teeth of an Insectivore but still of the same essential nature. Such teeth are termed bunodont, whence the name *BUNODONTIA* (Gr. *βουνός*, a hill or mound) has sometimes been applied to this division. The Hippopotamus, the sole representative of the family HIPPOPOTAMIDAE, is nothing but an enormous Pig; it differs from the ordinary Pig in having all its toes of equal length, whereas in the true Pig the outer (second and fifth) toes are small and do not reach the ground. The Hippopotamus spends most of its time in rivers and swamps feeding on the reedy vegetation of such places. It has exceedingly powerful jaws and when wounded has been known to crush a canoe between them. The true Pig belongs to the family SUIDAE and is a domesticated variety of the Wild Boar, *Sus scrofa*, which, as is well known, survived in England until the middle ages and still exists in Europe. In the male the canines, or eye-teeth, are powerfully developed, those of the lower jaw projecting upwards outside the mouth. In the Babirusa, *Babirusa alfurus*, of Celebes, the upper canines do not enter the mouth but are bent upwards and pass through special holes in the skin, curving back over the head like horns. They grow persistently, their roots being kept open. The Pigs are not strictly vegetable feeders but are really scavengers, eating every vegetable or animal substance they encounter, the food they seek especially consisting of roots. A very interesting genus, the Peccary, is represented by two species, *Dicotyles tajaçu* and *D. labiatus*, which inhabit the American continent. The former ranges from Patagonia to the Red River of Arkansas, the latter between Paraguay and British Honduras. The name means "two navels" and was suggested by the presence of a large gland in the middle of the back resembling a navel. On the hind-foot the fifth toe is wanting, so that there are only three toes; but the position of the axis of symmetry is still between the third and fourth toes. The Peccaries go in droves and are most dangerous antagonists; climbing a tree is the only chance of safety to a hunter who meets a herd.

Ruminantia.

When we leave the Pigs we have to deal with the higher section of the Artiodactyla, the *SELENODONTIA* or *RUMINANTIA*, which include most of our domestic animals, the Cow, Sheep, Goat, Camel, etc., as well as all the Deer and Antelopes. The latter name is derived from the habit of ruminating, that is of bringing the food back from the stomach into the mouth after it has been swallowed and chewing it again. Corresponding to this habit we find that the stomach has acquired a complicated structure. Just where the gullet opens into it we find a large pouch projecting laterally with the walls covered with little projections or

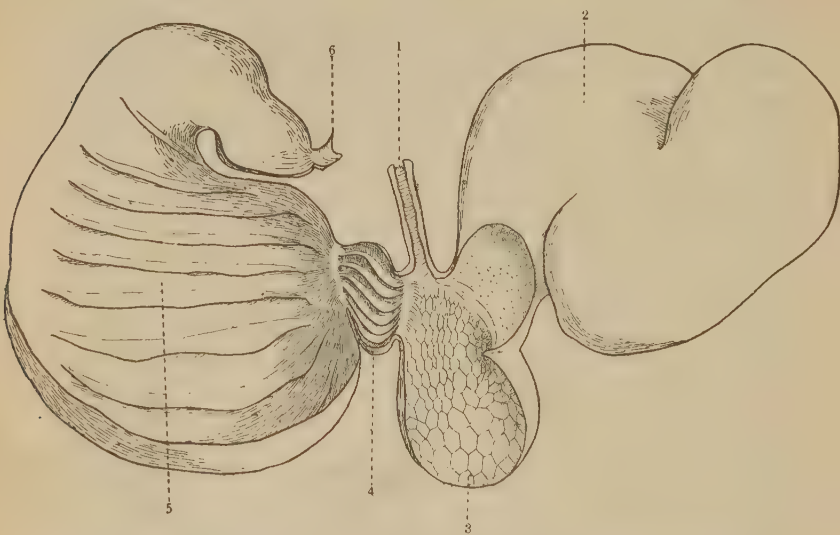

FIG. 346. Stomach of a Sheep, cut open to show the various chambers.
1. Oesophagus. 2. Rumen. 3. Reticulum. 4. Psalterium. 5. Abomasum. 6. Duodenum.

papillae; this is called the paunch or rumen. Just below the oesophagus is another smaller pouch divided by a constriction from the first (Fig. 346). The second pouch is called the reticulum because its walls are raised into intersecting folds producing cavities like the cells of a honeycomb. The food mixed with saliva is swallowed without chewing, and after traversing the oesophagus it is driven from rumen to reticulum and back by the action of the muscles and well soaked with gastric juice. After some time it is pressed up again into the mouth and thoroughly ground up by the great broad premolar and molar teeth. When swallowed for the

second time it is nearly fluid. It now passes down a groove or channel in the side of the gullet enclosed between two ridges. Reaching the spot where the gullet opens into the stomach, the grooves are continued along the upper wall of the stomach and the

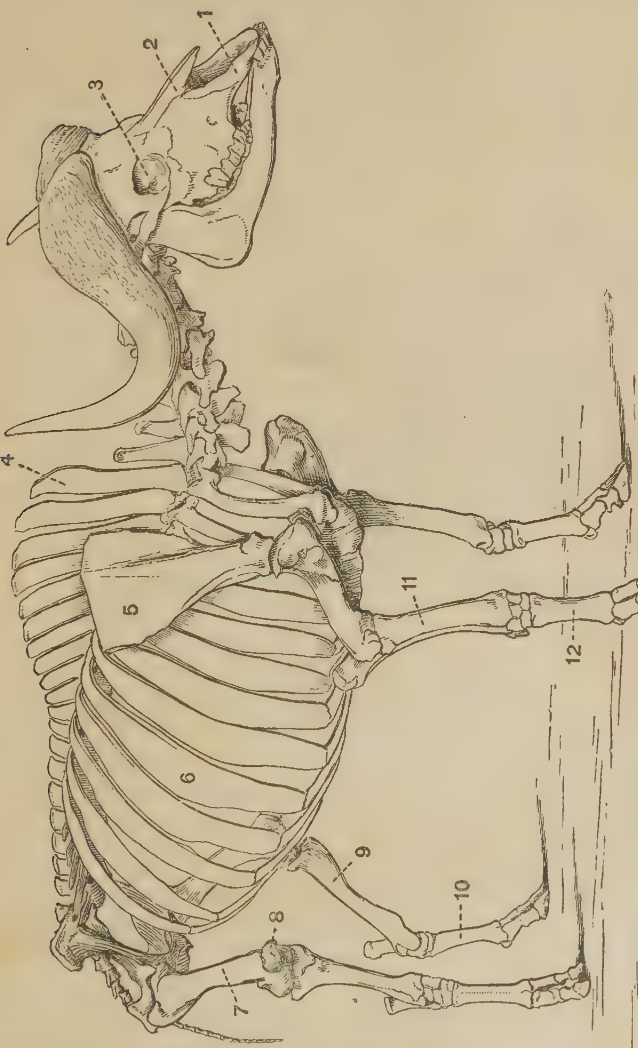

FIG. 347. Skeleton of a Cape Buffalo, *Bubalus caffa* × $\frac{1}{17}$. The left scapula is omitted for sake of clearness. 1. Premaxilla. 2. Nasal. 3. Orbit. 4. Neural spine of first thoracic vertebra. 5. Scapula. 6. Rib. 7. Femur. 8. Patella. 9. Tibia. 10. Metatarsals. 11. Radius. 12. Metacarpals.

fluid food is led away from the paunch into the third division of the stomach, the manyplies or psalterium, which has numerous folds of membrane projecting into its cavity; by means

of these the food is completely filtered from all the solid matter it contains. It then passes on into the fourth and last compartment, the abomasum, whose walls are raised into but a few ridges and which is lined with an epithelium containing numerous gastric glands. This leads into the duodenum or first part of the intestine, in which the digestion is completed. The teeth of the Ruminants have no distinct tubercles like those of the Pig, since these projections have become confluent so as to form hard curved ridges of enamel; and as the jaws shift on each other sideways, the upper and lower back teeth produce a grinding action just as two millstones do. The name *SELENODONTIA* (Gr. σελήνη, the moon) has been given to the Ruminantia on account of the crescentic ridges on their teeth, which are termed selenodont. It is interesting to note as evidence of the more advanced structure of the Ruminantia as compared with the Suinae, that the selenodont teeth always pass through a bunodont stage in their development. The canines in the upper jaw are long in the male *Moschus*, who no doubt uses them in his fight for the possession of the female. The lower canines however are usually placed close to the lower front teeth and are indistinguishable from them. There are—with few exceptions—no front teeth in the upper jaw, and the grass is bitten off by pressing the lower front teeth against a patch of hardened gum.

The feet of the Ruminants are organs beautifully formed for quick motion; the ideal which Nature has so to speak striven to attain being the same in their case as in that of the Horse, though she has had to start from a different basis. As in the case of the Horse, the end in view has been a firm jointed lever moving only in one plane; but in Ruminantia this has been attained by keeping two fingers and two toes and so to speak glueing them together except in the bones of the hoof. Ruminants, like Horses, walk on the points of their finger- and toe-nails; the metacarpals of the third and fourth digits are fused together, while of the outer fingers and toes only vestiges remain which hardly ever reach the ground, and often do not appear externally. The "cloven hoof" is therefore formed by the nails of two fingers or two toes (Fig. 347).

Classification.

The families composing the division Ruminantia are the TRAGULIDAE or Chevrotains; the CAMELIDAE or Camels (Tylopoda); the CERVIDAE or Deer; the GIRAFFIDAE or Giraffes; the ANTILOCAPRIDAE which has but one species, the Prong-buck, *Antilocapra americana*; and the BOVIDAE or

hollow-horned cattle (Cavicornia) including Antelopes, Goats, Sheep and Oxen.

The TRAGULIDAE comprise some small animals found in Africa and India, in which the foot is intermediate in structure between that of the Pigs and that of the higher Ruminants: the outer toes are complete although very slender, and the two inner imperfectly joined with one another. The stomach and teeth however are like those of a Ruminant, except that there is no third compartment or psalterium. The African Chevrotain from the West Coast is

FIG. 348. The African Water-Chevrotain, *Dorcatherium aquaticum.*

larger than its Asiatic allies (Fig. 348). It frequents water-courses and is said to have the habits of a Pig.

The CAMELIDAE are familiar to all as far as their general appearance is concerned. The humps—of which the Arabian Camel, *Camelus dromedarius*, has one, and the Bactrian or Asiatic Camel, *C. bactrianus*, two—are masses of fat, reserve material on which the animal supports its life when deprived of food. In the foot the main weight rests on a pad behind the hoofs; these latter are separated from each other, so that the animal has a broader support than a Cow or a Deer. A Camel does not walk on its finger- and toe-nails,

but on the last joints of the fingers and toes. The stomach has no psalterium, but both the rumen and reticulum have a large number of water-cells, that is deep pouch-like outgrowths in which a quite undrinkable fluid is stored. It will be noted that all the peculiarities of the structure of the Camel which have just been mentioned are directly related to the exigencies of a life on arid, sandy wastes. Thus the diverging toes and leathery pad on the foot enable them to secure a broader surface of the yielding sand on which to support the animal's weight: the humps are a provision of food and the water-cells in the stomach contain a supply of fluid to serve the animal in its long wanderings from oasis to oasis over the desert. The Arabian Camel is only known in the domesticated state, but the Bactrian Camel ranges wild over some of the more inaccessible regions of Central Asia.

It is a remarkable and interesting fact that we find some members of the Camel tribe in South America. These animals, the Llama, *Auchenia glama*; the Vicuna, *A. vicugna*; the Alpaca, *A. pacos*; and the Huanaco, *A. huanacos*; live in the Andes. They have no humps but possess long fleeces which are used for making cloth. The skeleton of one of these animals is almost indistinguishable from that of a Camel, and they have the same stupid, stubborn ways as their relatives in the Old World. It is curious to see in the stomach the same provision as is found in the Camel, although water is, as a rule, plentiful enough where the Llama lives.

The higher Ruminants are divided into two main groups according to the character of their horns. In the CERVIDAE or true Deer the horns are bony outgrowths of the frontal bones. The horns are shed every year and are nearly always branched. They may be termed antlers to distinguish them from the true horns of the Bovidae. The antlers are usually confined to the male, but in the Reindeer, *Rangifer tarandus*, which is called the Caribou in Canada, they also occur in the female. When the antler has attained its full growth the blood supply ceases and the skin peels off. In a rim round the base called the "fur" absorption takes place, so that the greater part is easily detached. In the Cavicornia or BOVIDAE, the core of the horn is an unbranched bony outgrowth into which air spaces continuous with the cavity called the frontal sinus of the skull often extend. This core is permanent and is covered by a hard horny sheath made of compacted hairs. Two small families occupy an intermediate position, these are the GIRAFFIDAE, represented by the Giraffe, *Giraffa camelopardalis*, and the Okapi, *Okapia johnstoni*,

and the ANTILOCAPRIDAE represented by the Prong-buck, *Antilocapra americana.* The Giraffe is now confined to the Ethiopian region; it is a conspicuous inmate of zoological gardens, on account of its extraordinarily long neck, in which however there are as usual only seven vertebrae. The Giraffe has two short horns, unbranched and covered throughout with soft fur and also the rudiment of a third median horn in the form of a projection of the nasal bones. The Okapi is a forest Giraffe with a comparatively short neck. In the Prong-buck, which is found on the prairies of North America, the horn bears a small lateral branch and is covered with a horny sheath, and this sheath, but not the horn itself, is shed once a year.

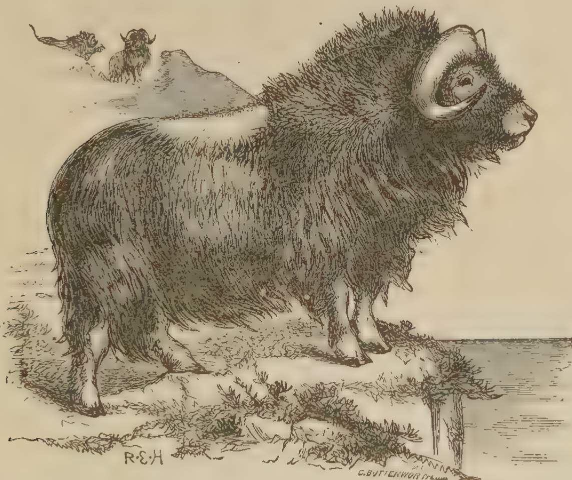

FIG. 349. The Musk-Ox, *Ovibos moschatus.*

In the family BOVIDAE is included everything from an Antelope to an Ox, and, strange as it may appear, we have practically a complete series of links filling up the gap between the graceful light-limbed Gazelle and the thick-necked Buffalo, so that we cannot say very precisely where Antelopes end and Oxen begin. The Musk-ox, *Ovibos moschatus* (Fig. 349), which ranges over the Arctic wastes of Canada in large herds, is intermediate in some respects between the Sheep and the Goats on the one hand and the Oxen on the other, but is more closely allied to the former series.

At present in Britain there are but two indigenous species of Deer found wild, the Red-deer of Scotland, *Cervus elaphus,* and the

Roe-deer, *Capreolus capraea*; the Fallow-deer, *C. dama*, is probably an introduced species, and at present is only represented in Britain by semi-domesticated animals. In Roman times there were wild Oxen, and some suppose that a breed of wild Oxen kept at Chillingham in Northumberland and in one or two other large parks are descended from these ancestors.

In Canada a large variety of the Red-deer, the Wapiti, *Cervus canadensis*, is found, also the Reindeer or Caribou, *Rangifer tarandus*, and the Elk or Moose, *Alces machlis*, with short bull-like neck and broad fan-like horns. Throughout the whole of Eastern America the so-called "Red-deer," *Cariacus virginianus*, is found in the mountains. The Bovidae are represented by the Musk-ox, *Ovibos moschatus*, with horns curved like a ram, and by the Rocky Mountain Goat, *Haploceros montanus*. Until recently the American Bison, the so-called "Buffalo," *Bison americanus*, ranged in enormous herds over the Western plains of North America; but before 1883,—with the exception of a few scattered stragglers which are "protected,"—this magnificent animal had been exterminated.

Until the introduction of modern fire-arms the Artiodactyla were in their way as successful and rapidly evolving a group as Teleostean Fish or as Birds. In a comparatively short time, however, all except the domesticated breeds or species specially preserved for sport will be exterminated. As it has been discovered that they harbour in their blood the dreaded parasite which causes sleeping-sickness it is probable that in regions infested by this disease their preservation for purposes of sport will be of short duration. In Tertiary rocks numerous families of extinct Ungulates are found which completely fill the gaps existing between Suidae and Tragulidae on the one hand and Tragulidae and Bovidae on the other.

Order VII. **Sirenia.**

The Sirenia or Sea-cows agree with the Cetacea or Whales in the manner in which they are adapted to an aquatic life. Thus all trace of hind-limbs has been lost, a pair of bones representing the pelvic girdle alone remaining, the fore-limbs have become flippers, the tail is broadened and there is a tail fin with horizontal flukes. Underneath the skin there is a thick layer of fat and the hairy coat is reduced to a few scanty hairs scattered over the skin. The lips, however, are covered with numerous thick bristles. The nasal organ is rudimentary. Apart from these resemblances which are due to

adaptation to a similar mode of life, the Sirenia differ from the Whales so profoundly that no direct relationship can be assumed to exist between the two groups. The Cetacea are all flesh-eaters but the Sirenia are vegetable feeders and browse on sea-weeds and other water-plants. As these habits necessitate their staying under the

FIG. 350. Skull of African Manatee, *Manatus senegalensis* × $\frac{1}{5}$.

water for some considerable time, the bones are heavy and solid, quite different in structure from the bones of Whales, which are much more spongy in texture. The skull is long, not rounded, and the face bones are only moderately developed. The parietals are

FIG. 351. Front view of head of American Manatee, *Manatus americanus*, showing the eyes, nostrils and mouth. A. with the lobes of the upper lip divaricated. B. with the lip contracted. From Murie.

not pushed aside by the development of the supra-occipital; the supra-orbital plate of the frontal is small, while the orbit is large and bounded below by a very powerful jugal. The teeth are broad

and crushing, and front teeth sometimes are found developed as tusks. There is no such snout as is found in Whales, but there are large movable lips by means of which food is seized (Fig. 351). The teats are placed on the breast as in Bats, and the mother when nursing supports the young with its head above water by means of the flipper which is more flexible than the flipper of a Whale. It has been suggested that the tails of Mermaids may have been suggested to sailors by the sight of these strange mothers holding their pups on their arms. There are two genera: (1) *Manatus*, the Manatee found in the warmer parts of the coastal waters of the Atlantic and in the estuaries of its rivers both in America and Africa, and (2) the Dugong, *Halicore*, found all around the coasts of the Indian Ocean and round Australia where it is fished for and eaten. Until 1768 a third species, *Rhytina stelleri*, of great size, 20—25 ft. long, inhabited some islands in the Behring Sea. It had no teeth, their place being supplied by horny plates on the gums. This species was exterminated by Russian hunters. Remains of extinct species of Sirenia with front teeth and vestigial hind-limbs have been discovered and the structure of these renders it probable that Sirenia are descended from some primitive Ungulate allied to the Eocene ancestor of Elephants.

Order VIII. **Rodentia.**

The Rodentia or Gnawers (Lat. *rodo*, to gnaw) are another of the main divisions of the Mammalia and include our Rabbits, Hares, Squirrels, Rats and Mice, besides the Porcupine, Beaver, Guinea-pig and many other foreign species. These are all sharply marked off from other mammals by the structure of their teeth. The incisors, of which there are typically only one pair in each jaw, are chisel-shaped and covered with hard enamel on their outer sides only. They constantly grow and are only kept down to proper size by continual gnawing and rubbing against each other (Fig. 352). If one of the teeth is destroyed the opposite one grows until it may pierce the other jaw, prevent the mouth from being opened, and thus starve the animal to death. There are no canines, so that there is a great space or diastema between the front teeth and back teeth. The claws are always blunt and nail-like, and walking is done on the last joints of fingers and toes, not as in the case of the Ungulates on the points of the nails (Fig. 322). Our English Rodents are the Hares and Rabbits, LEPORIDAE; the Squirrels,

SCIURIDAE; the Voles, Rats and Mice, MURIDAE; and the Dormouse, the sole British representative of the family MYOXIDAE. In North America there are allied species, and in addition the Ground-squirrels, or Chipmunks, *Tamias*, and three species of Woodchuck or Marmot, *Arctomys*; also Porcupines, represented by the common Canadian Porcupine, *Erethizon dorsatus*, the Beaver, *Castor canadensis*, and many others. *Hystrix cristata* is the Porcupine of Southern Europe and Northern Africa. The Guinea-pig is probably a domesticated variety of the South American species *Cavia cutleri.*

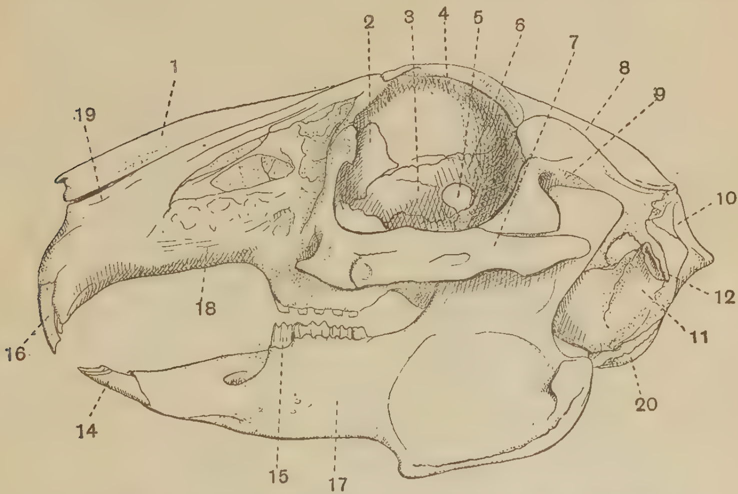

FIG. 352. Side view of the skull of the Rabbit, *Lepus cuniculus.*

1. Nasal bone. 2. Lachrymal bone. 3. Orbitosphenoid. 4. Frontal. 5. Optic foramen. 6. Orbital groove for ophthalmic division of trigeminal nerve. 7. Zygomatic process of squamosal. 8. Parietal. 9. Squamosal. 10. Supra-occipital. 11. Tympanic bone. 12. External auditory meatus. 14. Lower incisor. 15. Anterior premolar tooth. 16. Anterior upper incisor. 17. Mandible. 18. Maxilla. 19. Premaxilla. 20. Occipital condyle.

These various species are very like each other in their general anatomy, but differing in the character of their molars, in their fur and in their tails.

Hares and Rabbits constitute the *DUPLICIDENTATA*, one of the two sub-orders into which the order is divided. The name is derived from the possession of an extra pair of upper incisors, which however are so small as to be useless. The tail is short and the cusps of the premolar and molar are joined so as to form ridges or folds running across the tooth. The Common Hare,

Lepus timidus, and the Mountain Hare, *L. variabilis*, are both British; they have longer legs than the third British form, the Rabbit, *L. cuniculus*, and have fewer young at a time. In the temperate part of North America there are at least six species of Duplicidentata all referable to the genus *Lepus*. Of these the most interesting are *Lepus americanus* and *Lepus campestris*. The fur of both these species turns white at the tips in winter, enabling the animals to escape observation on the snow-covered ground.

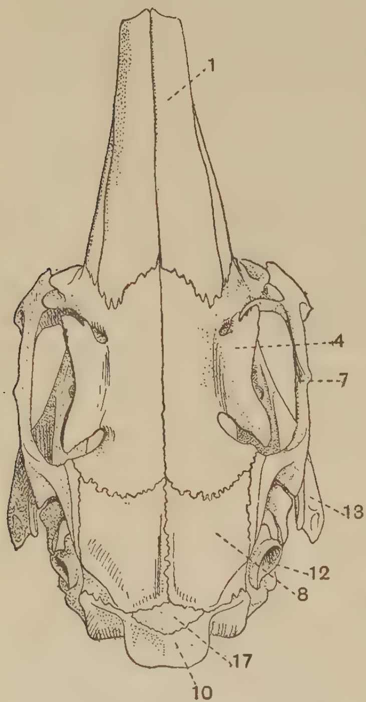

Fig. 353. Dorsal view of the skull of a Rabbit, *Lepus cuniculus*.

1. Nasal bone. 4. Frontal. 7. Process of squamosal supporting the jugal. 8. Parietal. 10. Supra-occipital. 12. External auditory meatus. 13. Angle of lower jaw. 17. Interparietal.

L. americanus, the Northern Hare, is abundant in New England and Eastern Canada: its summer fur has a cinnamon colour. *L. campestris* is the famous "Jack-Rabbit" of the western prairies, which has fur of a yellowish-gray colour in summer. It can run with great swiftness.

The remaining Rodentia are called *SIMPLICIDENTATA*, and possess only two incisors above, one on each side.

The Squirrels, SCIURIDAE, are distinguished by their bushy tail, their large hind-limbs and the fact that the cusps on their back teeth are distinct. *Sciurus vulgaris* is the common British Squirrel; it extends from Ireland to Japan. Two species are very common in Canada and New England, viz., *Sciurus hudsonicus*, the Red Squirrel, and *S. carolinensis*, the Gray Squirrel. These lively little animals can be seen in autumn disporting themselves in the trees lining the avenues of the suburbs of Montreal. *Sciuropterus volans* is the Flying Squirrel; this animal is provided with a furry expansion of the skin of its sides joining the elbow and knee. This expansion

forms a parachute-like membrane which supports it in its great leaps from tree to tree. In these manœuvres it is assisted by the broad flattened tail. The Flying Squirrel is common in the temperate part of the United States. A similar but larger species (*S. sabrinus*) may be seen at dusk leaping from tree to tree on the Mountain of Montreal. *Anomalurus*, found in West and Central Africa, is also called a Flying Squirrel, since the skin of its sides is prolonged into a parachute-like membrane (Fig. 354). It differs from *Sciuropterus* however, in having a round tail provided with horny scales underneath, which assist in climbing, and in having its "parachute"

FIG. 354. The African Flying Squirrel, *Anomalurus fulgens*.

supported by a cartilaginous rod arising from the elbow. In reality *Anomalurus* is a surviving member of a primitive group of Rodentia termed PROTROGOMORPHA, intermediate in character between Squirrels and Mice, most of which are extinct.

The Mice and Rats, MURIDAE, have naked tails with scales underneath. The ordinary Rat is the brown Norway Rat, *Mus decumanus*, which was introduced some time ago into England and had almost everywhere driven out the old English Black Rat, *M. rattus*. Of

recent years however this latter species has increased its numbers and it is now holding its own. The Common British Mouse is *M. musculus*: the Wood-mouse, *M. sylvaticus*, and the Field-mouse, *M. minutus*, also occurs in Britain. The Water-rat or Vole, *Arvicola*, is distinguished from the true Rat by the fact that the cusps on its back teeth, instead of being rounded as in the true Rat, are angular. *A. amphibius*, the Water-vole, *A. agrestis*, the Field-vole, which often does much damage to crops, and *A. glareolus*, the Bank-vole, represent the genus in Britain. The Dormouse, *Muscardinus avellanarius*, which like the Squirrel passes the winter in a hole in a tree, has a long bushy tail, and, in outward appearance at any rate more

FIG. 355. The Musquash, *Fiber zibethicus*.

resembles a tiny Squirrel than a Rat. In its skull it resembles the MURIDAE, but it differs from both Squirrels and Rats in not possessing a caecum on the intestine. On this account it, along with five or six allied species from Europe and Africa, has been separated as a distinct family, the MYOXIDAE.

Amongst the most interesting American Rodents are the Beaver, the Porcupine, the Ground-squirrel, the Marmots and the Musquash. The Beaver, *Castor canadensis*, sole representative of the family CASTORIDAE, has a broad flat tail, suited for swimming, which is covered with horny scales. The Beaver, by means of its sharp incisors, cuts down trees growing on the banks of streams, so that they fall across streams thus damming them up and raising the

level of the water so as to cover the entrance to their burrows. By this means large tracts of country have been converted into swamp. The Porcupines (HYSTRICIDAE) have some of their hairs developed into sharp spines which make them awkward objects to handle. In the Canadian Porcupine, *Erethizon dorsatus*, the spines are concealed by the fur. The commonest Ground-squirrel of North America is the Chipmunk, *Tamias*, an active little animal with large eyes and a short hairy tail. The Prairie Marmot, *Cynomys*, the so-called Prairie-dog or Ground-hog is also a Ground-squirrel with a very short tail. It lives in communities, burrowing in the ground and its home is often shared by a small burrowing Owl, *Athene cunicularia*, and by a Rattlesnake, which probably eats the young Marmots. The Musquash or Musk-rat, *Fiber zibethicus*, one of the MURIDAE, is peculiar to North America, and very widely distributed in suitable places (Fig. 355). It is aquatic, living on roots and water-plants and is most active at night. It constructs burrows in the banks of streams, the openings of which are under water. Its fur is valuable.

Order IX. **Cheiroptera.**

The Cheiroptera (Gr. χείρ, a hand; πτερόν, wing), or Bats, have not in their general organisation, in teeth or brain or stomach, departed far from the Insectivora; their great distinguishing feature is the modification of the arm into a wing. As in Birds, the fore-arm is bent up on the upper arm, the wrist bent down on the fore-arm; but unlike Birds' wings the flying membrane is of skin, the greater part of which is stretched between the fingers of the five-fingered hand, only the smaller part extending, as in Birds, between the elbow and the side of the body. The hand is enormous, the little finger being, as a rule, very greatly developed and as long as the rest, while the thumb alone is small and is not included in the membrane but ends in a hook-like nail (Fig. 356). Part of the membrane extends down the thighs, and in some even the tail is involved. The knees are turned outwards and backwards, a most extraordinary position which would mean dislocation if the hip-joint of any other Mammal were forced into it but which is rendered possible in Bats owing to the fact that in them the pubes are not directed inwards so as to meet one another in a symphysis but slope outwards and are consequently widely separated from one another (Fig. 356). When the Bat crawls it hooks itself along with its thumb-nail and pushes itself awkwardly with its hind feet. It has

a most awkward gait and the animal is consequently very helpless when not flying.

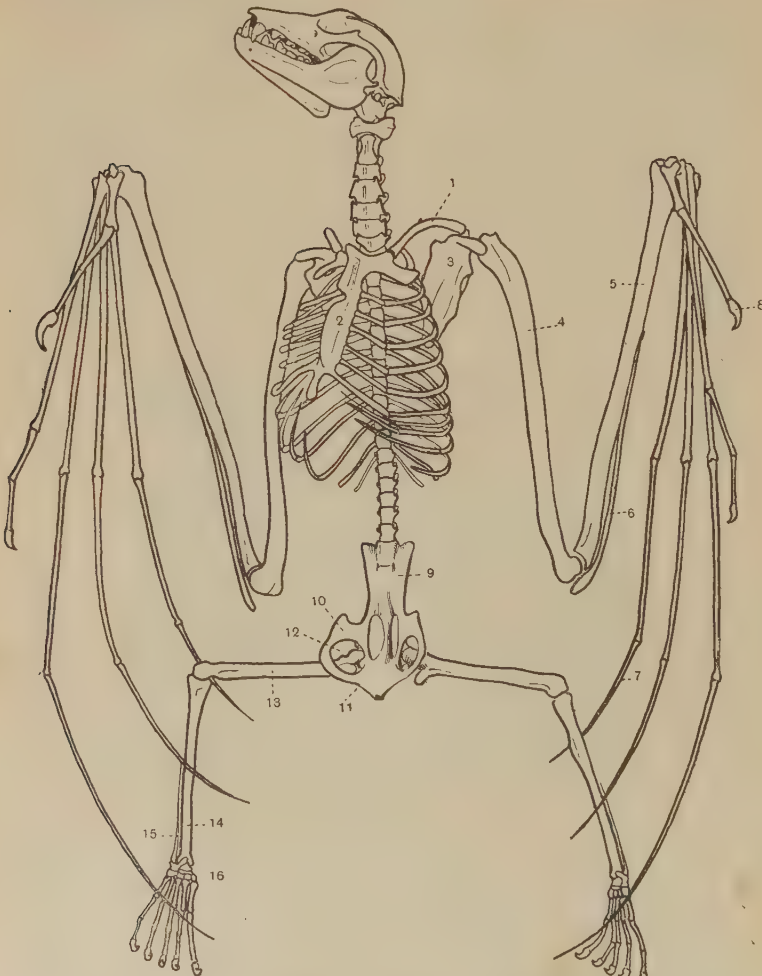

FIG. 356. Skeleton of *Pteropus medius*, a fruit-eating Bat × about ½.

1. Clavicle. 2. Keeled sternum. 3. Scapula. 4. Humerus. 5. Radius. 6. Ulna. 7. Little finger. 8. Thumb. 9. Ilium. 10. Pubis. 11. Ischium. 12. Obturator foramen. 13. Femur. 14. Tibia. 15. Fibula. 16. Tarsus.

One of the most extraordinary things about Bats is the development of sensitive patches of skin on the face for the purpose of perceiving faint disturbances in the air. It has been

shown that the eyes of Bats, although apparently normal, are really degenerate, that in fact the layer of visual rods in the retina, which is the special organ of light-perception, is most imperfectly developed. To compensate for this we find, in some species, the

FIG. 357. Female and young of *Xantharpyia collaris*. From Sclater.

outer ear, in others the skin around the nostrils, in others again the skin on the lips and chin, developed into curious outgrowths richly supplied with nerves. By means of these sense-organs Bats are enabled to avoid obstacles, and a blind Bat, let

loose in a room across which numerous strings have been stretched, will fly about without touching one. Owing to their powers of flight Bats are exceedingly widely distributed and extend to small oceanic islands where there are no other Mammals. The true Blood-sucking Bat or Vampire, *Desmodus rufus*, is found in Central and in South America. Its back teeth are rudimentary, but its front teeth are razor-edged. *Pteropus*, which includes the so-called Flying Foxes or Fox-bats of India and Madagascar, belongs to the family PTEROPIDAE; these are the largest Bats known; they feed exclusively on fruit, and the cusps on their teeth are blunter than is usual amongst Bats. The African *Xantharpyia*, one species of which frequents the interior of the Pyramids and other dark ruins in Egypt (Fig. 357) belongs to the same family. In Great Britain there are some fifteen species of Bat divided amongst five genera. Of these the Long-eared Bat, *Plecotus auritus*; the Whiskered Bat, *Vespertilio mystacinus*; the Horse-shoe Bats, *Rhinolophus hipposiderus* and *R. ferrumequinum*; the Barbastelle, *Synotus barbastellus*; and the Pipistrelle, *Vesperugo pipistrellus*; represent the genera. Besides the species just mentioned there are three more species of *Vesperugo* and three more of *Vespertilio* in Britain. South America has a large fauna of peculiar Bats, but the North American forms are allied to the British, although the species are distinct. The Serotine, *Vesperugo serotinus*, is the only species common to the two regions. *Scotophilus humeralis* is one of the most familiar species peculiar to North America.

Order X. **Primates.**

The last order of the Mammalia is that of the Primates, which includes Lemurs, Monkeys and Man. As was mentioned before, this order is characteristically arboreal, that is to say most of its members live among trees, climbing from branch to branch. This circumstance may explain why they retain certain primitive characteristics found elsewhere only amongst the Insectivora. Thus the thigh and upper arm are quite free from the body and the whole sole and palm are placed on the ground when walking; and there are five fingers and five toes. On the other hand the eyes are pushed round to the front of the skull instead of being placed at the sides of the head, and the jugal joins the postorbital process of the frontal, so that the orbit is surrounded by a bony ring (Fig. 358). Some at least of the toes have flat nails. The big toe is shorter than the rest,

and, except in Man, can be separated from them so as to be used for grasping. In most but not in all Monkeys the thumb can be used similarly, so that Monkeys are said to have four hands. There are two large mammae or nipples situated on the breast. Other mammae when present are vestigial and situated behind the functional ones.

There are two great divisions of the Primates, the *LEMUROIDEA* and the *ANTHROPOIDEA*. The first of these includes some curious little animals, of which the majority are found in the Island of Madagascar, the rest in Africa, India and the Malay Archipelago. Many of the species are nocturnal, move silently and have large eyes, whence the name Lemur (Lat. *lemures*, goblins, spectres). These animals have heads recalling those of rats, with no suggestion

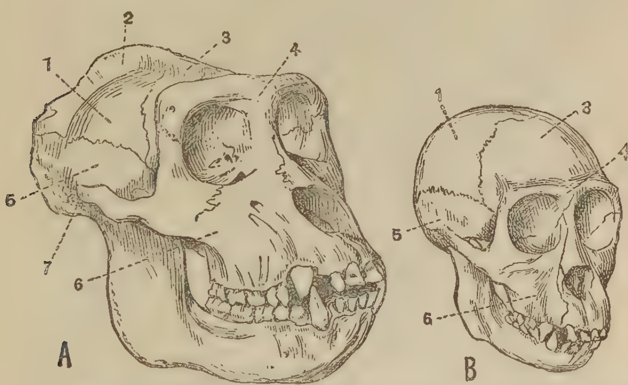

FIG. 358. Half front view of the skulls, A. of an old, B. of a young Gorilla, *Gorilla savagei* × ¼.

1. Parietal. 2. Sagittal crest. 3. Frontal. 4. Supra-orbital ridge. 5. Squamosal. 6. Maxilla. 7. External auditory meatus.

of the human face, and in their brains and some other points they are far below the Monkeys. The cerebral hemispheres do not cover the cerebellum; the placenta of the embryo is spread evenly all over the surface of the egg, and there are occasionally additional mammae on the abdomen. Their incisor teeth are separated in the middle line, but, as in all Primates, there are never more than two on each side. The Ring-tailed Lemur, *Lemur catta* (Fig. 359), is said to be an exception to the rule that the group is arboreal and to live amongst rocks and bushes, but other authorities say that it lives in troops amongst the forests of Madagascar. It is a gentle, graceful creature with a plaintive cry.

The *ANTHROPOIDEA*, including the true Monkeys and Man, are distinguished by the fact that the bony ring surrounding the orbit sends inwards a plate of bone, which completely separates the orbit from the temporal fossa. Further, the cerebral hemispheres conceal the cerebellum when the brain is viewed from above; the placenta is at first spread all over the surface of the egg but later becomes highly developed and concentrated on one part of the wall of the

FIG. 359. The Ring-tailed Lemur, *Lemur catta.*

uterus, and there are never more than two mammae. This sub-order of Primates is divided into five families, viz., HAPALIDAE, CEBIDAE, CERCOPITHECIDAE, SIMIIDAE, and HOMINIDAE, the last being constituted of the single species, *Homo sapiens*, Man.

The HAPALIDAE and CEBIDAE are confined to South and Central America, and are sometimes grouped together as *PLATYRRHINI* (Gr. πλατύς, broad; ῥίς, ῥινός, nose). The animals belonging to this

section have a broad internasal septum and three pairs of premolar teeth. The tympanic bone is without a tube-like prolongation. The HAPALIDAE or Marmosets are small, furry animals inhabiting the forests of Brazil and Columbia; they have the least ape-like feet of any of the Anthropoidea. The great toe is small and it

FIG. 360. The Orang-utan, *Simia satyrus*, sitting in its nest. From a specimen in the Cambridge Museum.

alone has a flat nail; all the other toes and all the fingers bear curved claws. There are only two pairs of molars. The CEBIDAE have flat or slightly curved nails on their fingers and toes and three pairs of molars, making with the premolars six cheek-teeth

on each side of each jaw, the largest number found amongst Anthropoidea. The Cebidae have prehensile tails which assist them in climbing. The genus *Ateles* includes the Spider-monkeys, in which this function of the tail is prominent, the under side of this organ being naked and scaly so as to allow the animal to obtain a hold. The genus *Cebus* has the tail hairy all round; several species of this genus are often seen in captivity.

The CERCOPITHECIDAE and SIMIIDAE are confined to the Old World. They constitute the section *CATARRHINI*, characterised by the possession of a narrow internasal septum, a spout-like prolongation of the tympanic bone extending into the base of the ear-flap, and the reduction of the number of premolar teeth to two pairs, whilst there are always three pairs of molars. The CERCOPITHECIDAE have the legs as long as the arms, or longer, and go habitually on all-fours. There are always bare patches of thick callous skin on the buttocks forming the so-called ischial callosities, on which the animals rest when they assume a sitting posture, and there is in almost every case a well-developed tail. This family includes the Indian and African monkeys, among them the Bandar-log of Kipling's Jungle Tales. One species, *Macacus inuus*, the Barbary ape, is found on the Rock of Gibraltar, and this is the only species which enters Europe. It is remarkable for being completely tailless. *Semnopithecus entellus* is the sacred Langur of India, and owing to its immunity from persecution has become very abundant.

The SIMIIDAE include those Monkeys which in structure and appearance most resemble Man. In this family the tail is completely absent, the arms are longer than the legs, and the gait might be described as that of a baby learning to walk. They never go completely on all-fours, but usually shuffle along unsteadily on their two feet, which like those of a baby show a tendency to turn inwards under them; they usually steady themselves by bending forward so that their knuckles touch the ground. Four genera are included in this section, viz. *Hylobates*, *Simia*, *Gorilla* and *Anthropopithecus*. *Hylobates* include several species known as Gibbons, inhabiting South-Eastern Asia and the Malay Archipelago. These are Apes with exceedingly long arms; they assume a completely upright position when on the ground and run along holding up their long arms in the air as if they were balancing poles. In their power of supporting themselves without resting the arms on the ground they approach Man; but in other respects they depart widely from him, as for instance in the brain, where the

cerebellum is not completely covered by the cerebrum. *Simia* is represented by a single species, *S. satyrus*, the Orang-utan, a large animal about $4\frac{1}{2}$ feet high, which is found in the islands of Borneo and Sumatra. This animal walks on two feet supporting itself on its knuckles. It lives however almost entirely in trees, constructing a sort of nest for itself out of branches (Fig. 360). It is remarkable for its high rounded cranium enclosing the large brain, which presents the closest approximation to the human brain of all the brains of Apes. The cranium is however still small compared to the bones of the face and lower jaw. Of the next genus *Gorilla* only a single species exists, viz. *G. savagei*, confined to a limited region of Equatorial Africa. This is the largest of all the apes, reaching a height of $5\frac{1}{2}$ feet. It is distinguished from *Simia* by its shorter arms and more receding forehead. The skull of the young Gorilla strikingly resembles a child's skull, but in the adult it is deformed by the development of great bony ridges which give attachment to the muscles of the face (Fig. 358). *Anthropopithecus* is represented only by *A. troglodytes*, the Chimpanzee, which lives in Western Africa in the same region as the Gorilla, but has a wider distribution. It is distinguished by its shorter arms, which do not reach below the knee, and by its smoother and rounder skull. It does not reach a height of more than 5 feet and is on the whole the most Man-like of all the Simiidae, though each of the other species of the family approaches more closely to the human standard in some particular feature and the Chimpanzee is more purely arboreal in its habits than the other Simiidae.

Man is distinguished above all by the great size of the brain, which is double the size of that of the highest Monkey, and by the modification of the leg so as entirely to support the body, in consequence of which the big toe is no longer used for grasping. Some hold that it was this latter modification which brought about the great development of the intelligence of Man, arguing that when once the hand was entirely at the service of the brain the varied uses to which it could be put would give the opportunity for the use of the mind. This seems probable, but the great factor which has stimulated the mental development of Man is his habit of living together in societies and undertaking concerted enterprises for the benefit of the community. To this power of combination not only intellect but also language and morals may eventually be traced back. Man did not make society, it was society that made Man. The general circumstances of the Evolution of Man are becoming

quite clear; just as the Marmot may be described as a ground-squirrel, so Man may be described as a ground-ape. In the warm Miocene Epoch a luxuriant forest covered a large part of Europe and Asia and in this forest Simiidae abounded, and remains of genera intermediate between the Gibbon and Chimpanzee have been found in France. In succeeding Pliocene and Pleistocene times the climate became colder, the mountains were covered with glaciers, the forest receded and was replaced by steppes over which roamed myriads of grazing animals. Under these circumstances, the more enterprising Simiidae descended from the trees and began to assemble in troops to chase the smaller animals they found on the plains and so Man was evolved. He is a product of the Glacial Epoch.

The Human species is divided into a great many races which are more distinct from one another than allied species in other groups of animals, but all of which so far as is known are more or less fertile amongst each other. They differ in the shape of the skull which may be broad (brachycephalic) or long (dolichocephalic) in the hair which may be curly, wavy or lanky, in stature and the proportions of the limbs. We cannot in this short treatise describe all these races; many of these such as the Esquimaux, the Bushmen and the Australians, are represented by small numbers and are dying remnants of primitive man, but we must briefly refer to the great dominant races which make up the bulk of the world's population. These are:

(1) The Negroes, dark skinned, dolichocephalic, curly haired people with thick skulls and weak ankles which form the bulk of the population in Equatorial Africa and also inhabit the larger islands of the Malay Archipelago where they are called Melanesians; they have never evolved a native civilization.

(2) The Mongols, yellow-skinned brachycephalic lanky haired people with slit-like eyes; these include all the Chinese and Japanese as well as the less civilized and wandering tribes of Siberia and the Malays who inhabit the Western part of the Malay Archipelago. The natives of North America or Amerinds are supposed to be an offshoot of this race distinguished by an arched nose and slit-like nostrils.

(3) The Alpine race, brachycephalic people with lanky or wavy hair, short in stature, a race resembling the Mongols but distinguished by lighter complexion and abundant hair. This race originated in Western Asia but invaded Europe in prehistoric times subjugating the previous inhabitants. They form the bulk of the people of central Europe; the Russian and German peasantry as also those of

central France belong to this race and they have contributed to the population of the British islands.

(4) The Mediterranean race, swarthy skinned dolichocephalic people with wavy hair and dark eyes, the original inhabitants of Europe in post-glacial times and the first race to evolve a civilization. To this race belong the Arabs, the ancient Egyptians, as well as the modern peasantry of that country, the Southern Italians, the Spanish, Portuguese and Moors, and the Bretons and Gascons in France, and the small dark people of Wales, Cornwall, the Western Highlands and Ireland.

(5) The Nordic race, fair skinned dolichocephalic people with wavy hair and blue eyes. This race originated near the Baltic and spread south conquering and organising the whole of Europe. It represents not only a large and virile section of the population but the aristocracies and ruling houses of Europe. To it belonged (*a*) The "heroic" Greeks who fought at Troy and the "Dorian" founders of Sparta. (*b*) Probably also the ancient "Patrician" families of Rome. (*c*) The Goths, Germans and allied Barbarians who overran and conquered the Roman Empire. (*d*) The Saxon invaders of Britain. (*e*) The Norman invaders of Britain and Europe. In its purest form it is found at the present time in the Scandinavian Peninsula. Modern History may be said to be due to the initiative and prowess of this race. The Alpine race has developed craftsmanship, they were the first to use metal tools whilst the Mediterranean race evolved the ancient Egyptian civilization the oldest in the world.

The fossil representatives of the class Mammalia are exceedingly numerous. It would lead us too far to give even such a general account of them as was given of fossil Reptilia, but a few hints as to the light thrown by them on the ancestry of existing groups may be given here. Mammalia seem to have been derived from the early Reptilia of the Sandstones overlying the Coal Measures. One group of these, the Theromorpha, in showing the division of the teeth into three kinds, and in the envelopment of the quadrate by the squamosal, are now regarded as the ancestors of the class. Unfortunately the succeeding rocks are mostly of marine origin, and in them few and fragmentary remains of Mammalia are preserved. Some of these show small molars covered with many cusps similar to the teeth of *Ornithorhynchus* and these teeth are classified as the remains of an order MULTITUBERCULATA, the members of which are supposed, like *Ornithorhynchus*, to have had a reptilian arrangement of the genital organs. The remains are principally lower

jaws, but in one case a scapula with a facette for a coracoid and an interclavicle have been found which bear out the conclusions founded on the jaws. At the same time other jaws have been found which show teeth of a different kind. These have molar teeth of the tritubercular pattern, but the angle of the jaw is inflected and these have been referred to the Metatheria. As however the latter group owe some of their peculiarities to degeneracy it would be better to regard these jaws as remains of the direct forerunners of Eutheria from which the Metatheria represent a side line.

When we come to the sands and clays lying above the Chalk which constitute the Tertiary "rocks," we find in many localities a rich assemblage of remains of undoubted Mammalia of the Eutherian type. The oldest horizon or Basal Eocene shows remains of animals called Condylarthra and Creodonta. Both groups are small plantigrade animals, with 44 teeth, but in the first group the cusps of the tritubercular molars are blunt, and in the second sharp and pointed. In this small distinction the beginning of the cleft is seen which widens into the chasm now separating Ungulata and Carnivora. Modern Insectivora are the little modified descendants of the Creodonta, whilst the so-called "Sub-ungulata" may be regarded as survivors of the Condylarthra which have undergone modifications in their dentition. In the next horizon or Lower Eocene traces of the Primates appear as Lemuroidea, the marks discriminating them from Creodonta being the enlargement of the orbit and its surrounding ring of bone, while the molar teeth have a fourth tubercle. At the same time the Condylarthra begin to show Horse-like forms (*Phenacodus*), still with five fingers and five toes and of the Sub-ungulate type, but true Ungulata now appear with the bones of wrist and ankle in transverse rows and a reduced number of toes. The earliest of these, the Lophiodontidae, were Perissodactyla, and in the shape of the face some recall the Horse, others the Rhinoceros, though the limbs were like those of Tapirs. The cusps on the teeth were four in number, and were commencing to coalesce into ridges. Rodentia also make their appearance as Tillodontia, animals with one pair of large incisors in each jaw, but with the other incisors and the canines present; these forms are easily derivable from the Creodonta. The origin of the Artiodactyla becomes apparent in the next horizon, the Middle Eocene, a host of small Pig-like animals making their appearance which in higher formations gradually differentiate themselves into the families of Artiodactyla. The ancestors of the South American Edentata, which at the previous horizon were not separable from Creodonta except

by the fact that the tritubercular molars lost their enamel late in life, become at this period distinguished by the restriction of the enamel to bands and the reduction of the incisors. Still higher in the series Bats (Cheiroptera) make their appearance, little different from what they are at present.

In the horizon above this (Upper Eocene) the ancestors of Whales are found, as the Archaeoceti (*Zeuglodon*) with well-developed nasal bones, the nostrils placed about the middle of the snout, and with double-rooted serrated molar teeth, derivable from the tritubercular type by the development of additional cusps, all like the original three being in the same line. True Carnivora distinguished by the carnassials have likewise been by this time developed from the Creodonta; amongst the Ungulata the earliest forms of Camels and of Tragulidae have appeared, as well as the forerunners of Elephants and Sirenia.

Once formed, Carnivora rapidly become differentiated, for in the next period (Oligocene) Felidae and Viverridae had already appeared, and contemporaneously with them the first Deer (Protoceratidae) and the earliest Sirenia with visible hind-limbs (*Halitherium*). Still higher the Elephants (Proboscideae) appear represented at first by forms with both lower and upper tusks or even lower alone (*Mastodon* and *Dinotherium*). At the same time the Deer first appear with antlers and the Rhinoceros acquires a horn, and the family of Bears (Ursidae) is commencing to be distinct from the primitive Dog-like Carnivora, the gradual reduction in size of the premolars, and of the carnassial marking the change. True Apes (Anthropoidea) here succeed the Lemuroidea.

In the next period (Miocene) the Giraffe (*Samotherium*), *Hyrax* and *Orycteropus* appear and so practically the whole group of Mammalia has made its appearance, the remaining changes consisting chiefly in the extinction of many forms either completely, or partially, so that their representatives are now restricted to limited areas. It will be noted how completely the geological evidence bears out the idea of the central position of the group Insectivora among Mammalia.

The class Mammalia is divided as follows:

Sub-class I. Prototheria.

Mammalia which lay large eggs and in which the two oviducts are completely separated, and there is a persistent cloaca. No placenta.

Ex. *Ornithorhynchus*, *Echidna*.

Sub-class II. Metatheria.

Mammalia in which the young are born in a most imperfect condition, and are carried by the mother in a pouch on the abdomen. The oviducts are differentiated into vagina, uterus and Fallopian tube and the two vaginae are partially united. The cloaca is divided into an anus and a urino-genital aperture. An allantoic placenta may or may not be developed but when present is more or less vestigial. In all cases there is an umbilical placenta consisting of an adhesion between the yolk-sac of the embryo and the uterus.

Order I. **Polyprotodontia.**

Metatheria with four or five incisors on each side of the upper jaw and with at least three pairs of incisors of approximately equal size in the lower jaw.

Family 1. Didelphyidae.

Polyprotodontia with a large opposable great toe, the other digits of the hind-foot being subequal in size. American.

Ex. *Didelphys.*

Family 2. Dasyuridae.

Polyprotodontia with a rudimentary great toe, the other digits of the hind-foot subequal in size. Australian.

Ex. *Thylacinus.*

Family 3. Peramelidae.

Polyprotodontia with a rudimentary great toe, the other digits of the hind-foot united by a web of skin, the second and third being excessively slender: the muzzle long and pointed. Australian.

Ex. *Perameles.*

Family 4. Notoryctidae.

Polyprotodontia with rudimentary eyes, an enlarged manus and burrowing habits. Australian.

Ex. *Notoryctes.*

Order II. **Diprotodontia.**

Metatheria with not more than three incisors on each side of the upper jaw, and with, as a rule, one pair of large chisel-shaped incisors in the lower jaw, the other lower incisors being vestigial or absent.

Family 1. Epanorthidae.

Diprotodontia with all the toes of the hind-foot free from one another and subequal. American.

Ex. *Caenolestes.*

Family 2. Phascolomyidae.

Diprotodontia with the toes of the hind-foot united by a web of skin: only one pair of chisel-shaped incisors in upper jaw: limbs subequal. Australian.

Ex. *Phascolomys.*

Family 3. Phalangeridae.

Diprotodontia in which the toes of the hind-foot are united by a web of skin, the great toe being well developed, free from the web, and opposable to the rest, the second and third toes very slender: limbs subequal: three incisors on each side of the upper jaw. Australian and Papuan.

Ex. *Phalanger.*

Family 4. Macropodidae.

Diprotodontia in which the toes of the hind-foot are united in a web of skin, the second and third toes are slender and the great toe is rudimentary: the fore-limbs very short and suited only for grasping: three incisors on each side of the upper jaw. Australian and Papuan.

Ex. *Macropus*, *Bettongia*, *Petrogale.*

Sub-class III. Eutheria.

Mammalia in which the young are born able to suck and in which there is no pouch. The two vaginae are always completely confluent. The cloaca is divided into an anus and a urino-genital aperture. An allantoic placenta always present and greatly developed.

Order I. **Edentata.**

Eutheria devoid of enamel on the teeth and without median teeth; the limbs are, as a rule, provided with heavy hook-like claws; uterus simple and globular: placenta dome-shaped.

Family 1. Bradypodidae.

Limbs long and the fore-limbs considerably longer than the hind-limbs: muzzle short with few teeth: arboreal in habit. South American.

Ex. *Bradypus.*

Family 2. Myrmecophagidae.

Limbs short and stout: muzzle exceedingly long: no teeth. South American.

Ex. *Myrmecophaga.*

Family 3. Dasypodidae.

Limbs short and stout: face long with numerous teeth: a shield of dermal bones covered by horny scales. South American.

Ex. *Dasypus.*

Order II. **Effodientia.**

Eutheria resembling Edentata in teeth and claws but with bicornuate uterus and zonary or diffused placenta.

Family 1. Manidae.

Covered externally with large, overlapping horny scales: no teeth: long protractile tongue. Asian and African.

Ex. *Manis.*

Family 2. Orycteropodidae.

Covered with bristly hairs: teeth numerous and heterodont: no thumb on anterior limb. African.

Ex. *Orycteropus.*

Order III. **Insectivora.**

Small plantigrade Eutheria, with pointed cusps on the molar teeth: the brain of low type: a flexible snout often present. The more familar families are

Family 1. Erinaceidae.

Insectivora with the body covered with harsh spines: limbs subequal.

Ex. *Erinaceus.*

Family 2. Soricidae.

Small mouse-like Insectivora with soft fur.

Ex. *Sorex, Blarina.*

Family 3. Talpidae.

Mouse-like Insectivora with rudimentary eyes and large hands adapted to burrowing.

Ex. *Talpa, Condylura, Myogale.*

Order IV. **Carnivora.**

Eutheria with sharp recurved claws and powerful canine teeth: the premolars adapted for clipping flesh: the incisors small.

Sub-order 1. **Fissipedia.**

Carnivora with separated digits: a distinct carnassial tooth and one or more broad molars.

Family 1. Felidae.

Fissipedia with short face and a reduced number of premolar and molar teeth: with retractile claws.

Ex. *Felis.*

Family 2. Canidae.

Fissipedia with long face and full number of premolar teeth: claws non-retractile.

Ex. *Canis.*

Family 3. Ursidae.

Fissipedia with long face: teeth blunt and partially adapted for a vegetable diet: plantigrade in gait.

Ex. *Ursus.*

Family 4. Procyonidae.

Fissipedia with a sharp pointed muzzle and reduced number of teeth, otherwise like *Ursus.*

Ex. *Procyon.*

Family 5. Mustelidae.

Fissipedia with long necks and exceedingly flexible bodies: a reduced number of teeth: in the skull and in the shape of the carnassial tooth they resemble Ursidae but they are digitigrade in gait.

Ex. *Lutra, Meles, Mustela, Mephitis.*

Family 6. Viverridae.

Fissipedia with long necks and exceedingly flexible bodies; a reduced number of teeth, but the teeth are more numerous than in the Felidae. In the skull and the shape of the carnassial tooth they resemble the Felidae.

Ex. *Viverra.*

Sub-order 2. **Pinnipedia.**

Aquatic Carnivora with the toes united by a web of skin: the tail is rudimentary, but the two hind-limbs are turned backwards and closely apposed so as to form a paddle: no distinct carnassial tooth and no broad molars.

Family 1. Otariidae.

Pinnipedia still retaining a trace of the external ear, and capable of turning the hind-limbs forward so as to walk on land.

Ex. *Otaria*.

Family 2. Trichechidae.

Pinnipedia devoid of external ear, but capable of walking on land: the upper canines form long tusks.

Ex. *Trichechus*.

Family 3. Phocidae.

Pinnipedia devoid of external ear, and incapable of turning the feet forward, so that when on land they can only wriggle along with the help of their anterior limbs: the canines not specially enlarged.

Ex. *Phoca*.

Order V. **Cetacea.**

Large aquatic Eutheria which have lost the hind-limbs and have developed horizontal flukes on the tail. The fore-limb is a paddle: the cranium is globular and the teats are posterior.

Sub-order 1. **Mystacoceti.**

Cetacea devoid of teeth in the adult and with plates of whalebone in the mouth.

Ex. *Balaena*, *Balaenoptera*.

Sub-order 2. **Odontoceti.**

Cetacea with teeth at any rate on the lower jaw and no whalebone.

Ex. *Physeter*, *Globicephalus*, *Delphinapterus*, *Phocaena*.

Order VI. **Ungulata.**

Eutheria with limbs adapted entirely for progression, the terminal phalanx of each functional digit is enclosed in a short blunt nail.

Sub-order 1. **Sub-ungulata.**

Ungulata with short subequal toes, and with the bones of the carpus and tarsus arranged in parallel longitudinal series.

Family 1. Hyracidae.

Small Sub-ungulata with a very short snout: a pair of chisel-like incisors in each jaw.

Ex. *Hyrax* (*Procavia*).

Family 2. Proboscideae.

Large Sub-ungulata with a very long flexible snout (trunk) used for prehension: incisors long and curved, forming tusks: molars very broad, only one pair in use at a time.

Ex. *Elephas.*

Sub-order 2. **Ungulata vera.**

Ungulata in which the bones of the carpus and tarsus are arranged in transverse rows, the members of successive rows alternating with one another. The first digit is lost.

DIVISION I. PERISSODACTYLA.

Ungulata in which there is, with rare exceptions, an uneven number of digits in each limb, and in which the axis of symmetry passes through the third digit.

Family 1. Tapiridae.

Perissodactyla with four digits in the fore-limb and three in the hind-limb: a short flexible snout.

Ex. *Tapirus.*

Family 2. Rhinocerotidae.

Perissodactyla with three subequal digits in each limb: one or two median horns without bony cores carried on the nasal bones.

Ex. *Rhinoceros.*

Family 3. Equidae.

Perissodactyla with only one complete digit in both fore- and hind-limbs.

Ex. *Equus.*

DIVISION II. ARTIODACTYLA.

Ungulata in which there is almost always an even number of digits, and in which the axis of symmetry passes between the third and fourth digits, these digits being flattened against each other so as to form two symmetrical halves of a cylinder.

Section A. **Bunodontia** (Suina).

Artiodactyla with comparatively simple stomachs: the cusps on the molar teeth are separate.

Family 1. Hippopotamidae.

Large Bunodontia with four subequal toes in both fore- and hind-limbs.

Ex. *Hippopotamus.*

Family 2. Suidae.

Bunodontia of moderate size, in which the two outer toes though complete are shorter than the others.

Ex. *Sus, Babirusa, Dicotyles.*

Section B. **Selenodontia.**

Artiodactyla with complex stomachs adapted for ruminating: the cusps on the molars coalesce so as to form crescents.

Family 1. Tragulidae.

Small Selenodontia without horns, and with only three compartments in the stomach: the outer toes although excessively slender are still complete.

Ex. *Tragulus.*

Family 2. Camelidae.

Selenodontia without horns, with only three compartments in the stomach: the outer toes entirely absent, the inner toes slightly diverging below, the weight resting on a pad behind them.

Ex. *Camelus, Auchenia.*

Family 3. Cervidae.

Selenodontia with antlers in the form of bony outgrowths of the frontal bone shed annually: four compartments in the stomach: the second and fifth digits incomplete.

Ex. *Cervus, Cariacus, Capreolus, Rangifer, Alces.*

Family 4. Bovidae.

Selenodontia with horns which are outgrowths of the frontal, never shed, and covered with a thick horny sheath: four compartments in the stomach: the second and fifth toes rudimentary.

Ex. *Bos, Ovis, Ovibos, Haploceros.*

Family 5. Giraffidae.

Selenodontia with short horns which are outgrowths of the frontal, never shed, and permanently covered with soft fur, four compartments in the stomach: immensely elongated neck and very long limbs.

Ex. *Giraffa.*

Family 6. Antilocapridae.

Selenodontia with branched horns which are outgrowths of the frontal covered with a horny sheath. This sheath is shed annually but not the core of the horn. Four compartments in the stomach.

Ex. *Antilocapra.*

Order VII. **Sirenia.**

Aquatic Eutheria, with limbs and tail as in the Cetacea: the cranium is cylindrical and the teats pectoral.

Ex. *Manatus*, *Halicore.*

Order VIII. **Rodentia.**

Eutheria with one large pair of chisel-shaped incisors in each jaw growing throughout life and no canines. The Rodentia walk on the whole surface of the last joint of the digit, not on the extreme tip as do the Ungulata: the nails are blunt but not usually hoof-like.

Sub-order 1. **Duplicidentata.**

Rodentia in which there is a second pair of rudimentary incisors in the upper jaw.

Ex. *Lepus.*

Sub-order 2. **Simplicidentata.**

Rodentia in which there is only one pair of incisors in the upper jaw.

Ex. *Sciurus*, *Tamias*, *Mus*, *Fiber*, *Arvicola*, *Muscardinus*, *Castor*, *Erethizon*, *Hystrix*, *Cavia.*

Order IX. **Cheiroptera.**

Eutheria in which the fore-limb is converted into a wing, the hand being greatly enlarged and the fingers elongated in order to support the wing-membrane; the leg small and the knee-joint rotated backwards: teeth and brain resembling those of the Insectivora.

Ex. *Vespertilio*, *Vesperugo*, *Rhinolophus*, *Xantharpyia.*

Order X. **Primates.**

Eutheria with long limbs, the brachium and femur not being buried in the body: five digits in each limb, some of them

having flat nails: the great toe or thumb or both are opposable to the other digits. The orbits are rotated on to the anterior aspect of the skull and are completely surrounded by bone the brain is large.

Sub-order 1. **Lemuroidea.**

Primates in which the orbit is merely surrounded by a bony ring: front teeth separated by a space in the middle line.

Ex. *Lemur.*

Sub-order 2. **Anthropoidea.**

Primates in which the orbit is completely separated from the temporal fossa by an inwardly projecting sheet of bone: front teeth in contact in the middle line.

Section A. **Platyrrhini.**

Anthropoidea with a broad internasal septum, three pairs of premolar teeth and a simple tympanic bone: the great toe opposable to the other toes: the thumb imperfectly or not at all opposable to the other fingers.

Family 1. Hapalidae.

Small thickly furred Platyrrhini with a flat nail on the great toe only, claws on all the other digits: two molar teeth on each side.

Ex. *Hapale, Midas.*

Family 2. Cebidae.

Platyrrhini with flat or slightly curved nails on all toes: three molar teeth on each side.

Ex. *Ateles, Cebus.*

Section B. **Catarrhini.**

Anthropoidea with a narrow internasal septum, two pairs of premolar teeth and three pairs of molars in each jaw. The tympanic bone has a tube-like prolongation. The great toe is opposable to the other toes, the thumb imperfectly opposable to the other fingers.

Family 1. Cercopithecidae.

Catarrhini with arms not longer than their legs: bare

patches on the buttocks: with rare exceptions a well-developed tail.

Ex. *Macacus, Semnopithecus.*

Family 2. Simiidae.

Catarrhini with arms much longer than legs and a semi-erect gait: no tail.

Ex. *Gorilla, Hylobates, Simia, Anthropopithecus.*

Section C. **Hominidae.**

Anthropoidea with arms of moderate length and long legs: the foot entirely adapted to support the body, the great toe not opposable to the other toes: the thumb completely opposable to the other fingers: the upright attitude habitual: no tail: brain very large.

Ex. *Homo.*

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INDEX

Names of genera are printed in italics. The figures in thick type refer to illustrations. In all cases the references are to pages.

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